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PHYTOPATHOLOGY

VOLUME XII NUMBER 7

JULY, 1922

THE RELATION OF THE WATER PORES AND STOMATA OF THE POTATO LEAF TO THE EARLY STAGES AND ADVANCE OF TIPBURN.

B. F. LUTMAN

WITH FIFTEEN FIGURES IN THE TEXT.

The presence of hydathodes or water pores in the leaf of the potato plant seems to have been known for some time. They are mentioned incidentally by Jost (11, p. 57), in the following words: "Well known examples of the excretion of drops are furnished by the leaf apices of grasses, the leaf teeth of Fuchsia, Alchemilla, Brassica, and the potato." Clinton (3, p. 742–743) in discussing the advantages derived from spraying with Bordeaux mixture in years in which no blight appeared, suggested "that the results are largely due to the conservation of moisture in the leaves in dry seasons by clogging up the stomata and water pores with the sediment of the spray. The reasons for this belief are: (1) that the potato leaves, through their numerous stomata and terminal water pores, lose water very easily and are especially susceptible to what is known as tip burn in dry seasons; (2) that the unsprayed vines uniformly suffered earlier and more severely from tip burn than the sprayed, which were green for about two weeks after the unsprayed were dead; (3) That in 1910, which was a season like the preceding years, except with a little injury from blight at the very end of the season, spraying with Sulphocide and commercial lime-sulphur, sprays with comparatively little sediment, did not prolong the life of the vines or give increased yield, while spraying with Bordeaux mixture did."

It will be noted that the occurrence of water pores at the tips of the leaflets is merely mentioned by Jost, and by Clinton. Spanjer (22), in his list of plants known to possess water pores did not include the potato nor, in fact, any of the Solanaceae. Haberlandt (7, 9), in his extensive contributions to the comparative morphology of this type of plant excretory organs, did not refer to this group; neither does he mention

the potato in his long review of all the important literature in his "Physiological Plant Anatomy." Minden (14), in his list of plants known to possess some sort of an apparatus to secrete water, did not include the potato but did mention the following Solanaceae: *Solanum nigrum, Solanum dulcamara, Nicandra physaloides, Capsicum annuum, Datura laevis, D. stramonium.*

It would seem, therefore, that while it was commonly known that the potato plant was able under the proper conditions to exude water in the form of drops through some sort of water pores, no accurate study had been made of their form of arrangement. Indeed it is a moot point whether anyone heretofore has taken the trouble critically to examine the potato leaf in this respect. The attention of the writer was first called to them by the study of the venation of the leaf in its relation to the disease known as tipburn when apparently healthy leaves being prepared for the examination of the vascular system exhibited brown areas at their tips and sides in the center of which occured the water pores.

Before describing these organs and the arrangement of the veins on the potato leaf it seems advisable to review the descriptions of similar apparatus on other plants. It should be understood at the outset, however, that many points in the physiology of this water secreting apparatus are obscure and that the principles upon which they work are more or less a matter of conjecture and controversy.

Plant physiologists in general seem to agree touching the ecological uses of these organs better than they used to do concerning the methods by which those results are obtained. Practically all plants possessing water secretory organs are shade or semishade plants in their original habitat. Most of them grow in the tropics or subtropics. Because of the very heavy rains which occur in these regions, the plants at times are compelled to throw off the superabundance of water that has been brought up from the roots into the leaves, into an atmosphere already almost saturated with water vapor. Transpiration under such circumstances is necessarily small, the output is less than intake and a very high turgor exists throughout the plant, especially in the vessels which conduct the water. The only possible means of pressure release is the discharge of the water into the intercellular spaces of the leaves. However, such flooding of the air chambers leads to a decidely lessened exchange of gases and to curtailed starch assimilation. Futhermore, it has been suggested that retardation of transpiration and evaporation tends to slow down the upward current of soil water into the plant, to a considerable extent cut off the supply and, consequently, to lessen the crop.

The agreement is not so general among plant physiologists in regard

to the physicial agencies which bring about the extrusion of the water. Root pressure or bleeding pressure must furnish most of the force back of the passage of water through the walls of the tracheids, but Haberlandt is inclined to assign an important rôle to the epitheme cells which surround the vascular bundles of many varieties of plants, especially tropical species. This tissue serves not as a sieve, as might be the case if the root pressure was the sole force operative, but plays an active part in the control of the flow of the water which passes through it. The water must pass through these cells in order to enter the intercellular spaces and from them to flow into the water cavity under the guard cells and it is the function of these epitheme cells to maintain these intercellular spaces and cavity full of water. The large nucleus of the epitheme cells and their abundant supply of plasma is similar to that of the gland cells. Certain experiments of Haberlandt's seem to corroborate this conception of the function of the epitheme as a tissue.

The ability of the guard cells to open and close under different atmospheric conditions is doubtless a factor, but there seems to be some diversity in their mode of operation among such plants as *Secale cereale*, *Triticum vulgare* Vill., *Zea mays* L., etc.

The substitution of artificial pressure for root pressure was developed by de Bary (2) and Moll (15) but has been most extensively used by Haberlandt and Spanjer (22, p. 75). The method generally used was as follows: A branch of the plant was cut off and attached to the short arm of a J-tube and water or other liquids were forced into it by means of a mercury column 10 to 40 cm. in length, located in the longer arm, the plant in the meantime being kept under a bell jar lined with damp filter paper in order to curtail respiration as much as possible. Spanjer was able in this way to force water through the leaves in 2½ to 3 hours, but eosin solution and a 2.5 per cent solution of copper sulphate were 24 hours showing color in the drops.

The hydathodes were first noticed by the writer on potato leaves which he had prepared in order to examine the finer details of the vascular system, according to the method recommended by de Vries (25, p. 604–618). Other methods of rendering the leaf transparent and free from chlorophyll would probably give as good results but the following procedures will be found to be very successful with the potato leaf as, indeed, they have with most of the plants studied.

Boil the leaves for a few minutes in water, drain, soak for 12 to 24 hours in 95 per cent alcohol and then in a 5 per cent solution of sodium hydroxid for about the same length of time, wash in water for a few minutes, neutralize with a few drops of hydrochloric acid, place in 50

per cent glycerin for 24 hours, and then mount on a glass plate in pure glycerin. Small discarded photographic plates that have been cleaned are excellent for this purpose. Even very thick leaves are rendered so transparent that the entire leaf structure can be made out in optical

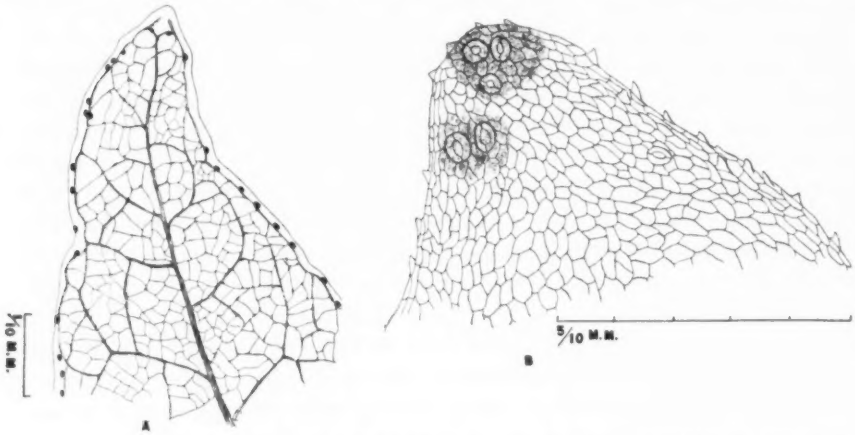

FIG. 1. A. Tip of very young leaflet showing venation and the position of the hydathodes. B. Tip of mature leaflet in surface view, showing groups of hydathodes. Dead tissue under the pores is indicated by dotting.

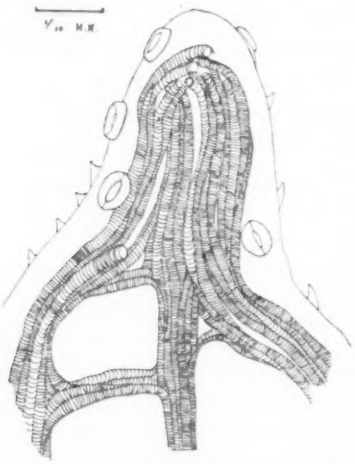

FIG. 2. Tip of leaflet, showing hydathodes and plexus of veins.

sections. An objective with long working distance is advisable, for example a Zeiss 16 mm. Apochromat with a No. 12 compensating ocular, or a Leitz $\frac{1}{7}$ inch objective combined with a No. 3 or 4 ocular

if the leaves were covered with a large ordinary cover glass. The venation as thus shown presents no marked peculiarities except in the regular occurrence of a very highly developed marginal vein. Artschwager (1) has made a very careful study of the anatomy of the potato plant with special reference to the structure and arrangement of the vascular elements, but the marginal vein of the leaflets does not seem to have attracted his attention. A number of plants were examined to determine whether this vein is at all common, but aside from the potato the nasturtium alone showed this peculiarity. The lateral veins branch away from the midrib to form numerous anastomoses throughout the leaf, but particularly near its margin the anastomoses form an almost continuous vein. This vein disappears occasionally in folds of the leaf,

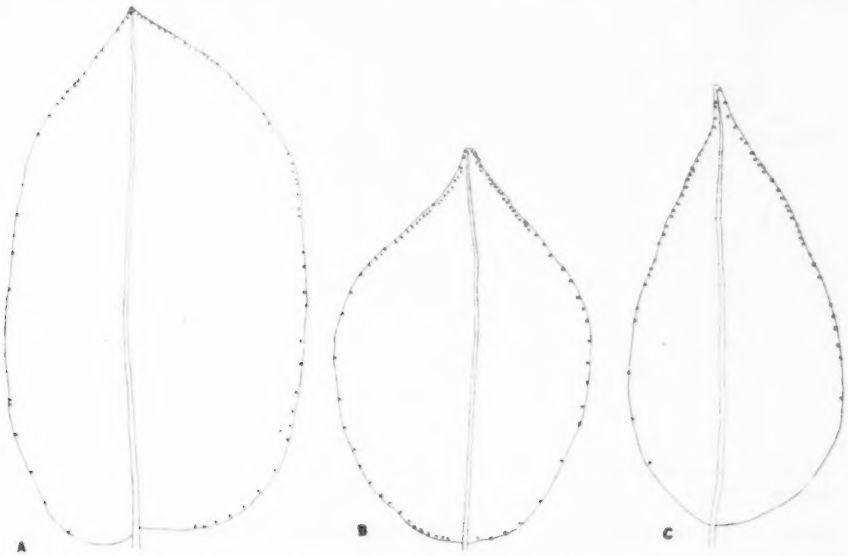

FIG. 3. Tip leaflets with position of hydathodes indicated. A and B are mature, C is a young leaflet.

but it is usually continuous for at least 95 per cent of the leaf margin.

It is composed of a varying number of tracheids and sieve tubes, the former sometimes being limited to a single large vessel, while in other places five or six tracheids may be observed. The development of this marginal vein is especially noticeable toward the tip of the leaf where it forms very important and large anastomoses with the vessels of the midrib (Figs 1, 2). In the extreme tip, (Fig. 2), the midrib and the marginal vein practically fuse to form a tangled mass of vessels,

many of which end blindly in the leaf parenchyma or under the water pores. On the basal portion of the leaflet, the marginal vein does not fuse with the midrib but runs parallel to it along the petiole, supplying the decurrent portion of the leaflet with vessels and sieve tubes. It is small in this region but it continues along this decurrent portion of the leaflet, joining by occasional small anastomoses with the midrib but continuing until it reaches the petiole of the succeeding leaflet where it forms the marginal vein. It will thus be seen that the marginal veins of all the leaflets are connected, forming a continuous series of tubes around the entire leaf.

Leaves taken from the field and examined in the manner described above, in June, 1921, showed brown areas over this marginal vein and

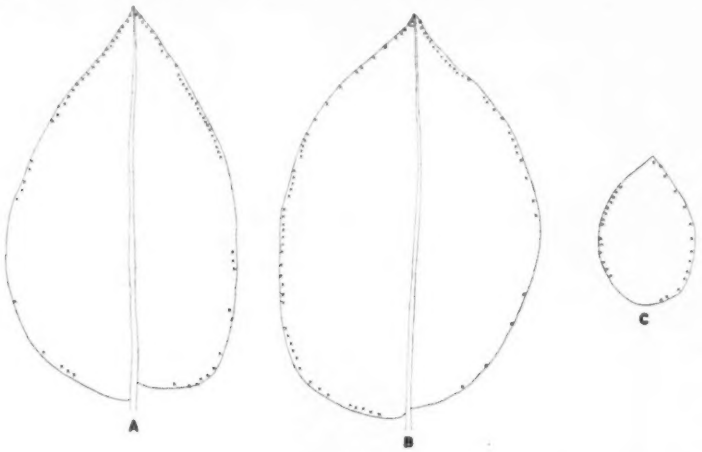

FIG. 4. A and B, side leaflets; C, a small intermediary leaflet. Hydathodes are indicated.

also at the extreme tip of the leaflet, whereas this condition had not been observed on those taken earlier in the spring from the greenhouse, which were apparently healthy and showed no signs of tipburn. A closer examination of these brown areas showed that a water pore much resembling the ordinary stoma was located above each one of these regions and was apparently the focus of the disturbance. All of these water pores were located on the upper margin of the leaf or opened out directly on the edge, but they always were in connection with the marginal vein. Whenever the marginal vein was suppressed, the water pores were also absent. A group of these organs was always clustered at the extreme tip of each leaflet on the upper side (Figs. 1, 2).

After these organs were observed on these older leaflets, many leaflets

of all ages and from different portions of the leaf were carefully studied under the microscope in order to determine their number and distribution (Figs. 3, 4). It was found that they occured on all the margins of the leaflets but that this distribution was somewhat irregular. The greater number per unit of leaf margin occured toward the tip, but they were present in even the basal lobes. A small number exist also on the very small leaflets located between the larger ones (Fig. 4, C). They average about 80 per leaflet, but one was found with 140. The number did not seem to vary much among the various leaflets although naturally the terminal leaflet, being usually a little larger, is likely to have more than the others.

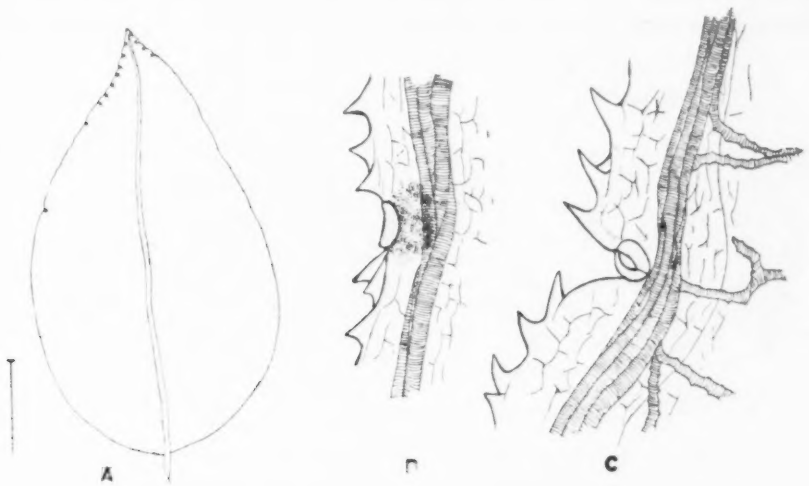

FIG. 5. A. Very young tip leaflet, true size indicated by line at the left: B and C are hydathodes in surface and partial sectional view.

Miss Rea (20) has found the hydathodes in *Campanula rotundifolia* more numerous and with larger pores on the shade shoots than on the sun shoots, as would be expected if these organs are to prevent the flooding of the internal tissues, since the danger is greater in such an environment where the transpiration is small. No attempt was made to compare the number on shade and sun potato leaves, but it is entirely possible that the high number was on a shaded leaflet.

The position of the hydathodes on the young leaflets differs somewhat from that on the older ones (Fig. 5). The young leaflets show a number of small infoldings of the margin, and it is in these curves that the hydathodes are to be found. At times the guard cells occur at the same

level as the surface, but more often they are located at the bottom of a little well formed by the margin of the leaflet (Fig. 4, C). They are much fewer in number than on the older leaflets and are limited to the tip region. The distribution of the hydathodes on a leaf about 2 cm. in length on the tip portion as shown in figure 1, A. The distribution on a leaflet of this length is very similar to that on a mature leaflet, and the small folds in the margin fill out so that the edge of the leaf is almost smooth.

The structure of the hydathodes as in sections (Fig. 6) is not unlike that of one of the stomata, but the water cavity is larger and opens directly on the vessels of the marginal vein as the epitheme, if such can be said to exist, is limited to a few scattered cells in no way very different from those of the immediately adjacent tissue. In stained sec-

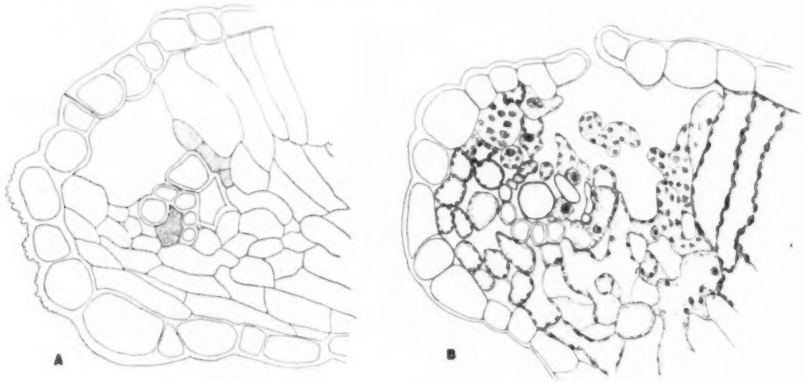

Fig. 6. A Hydathode from a section cut from fresh material; B, Hydathode from fixed and stained material.

tions (Fig. 6, B) the nuclei in the cells surrounding the vessels are unusually large and the cells are rich in cytoplasm, but there is no evidence that they are to be regarded as gland cells.

The relation of the hydathodes to the ordinary air stomata is an interesting one and is a part of the problem that has not been thoroughly worked out. It seems to have been avoided by the physiological morphologists who have studied these organs. Minden (14) followed the development of the water pores to some extent on the seed leaves of *Phacelia tanacetifolia*, *Solanum nigrum*, *S. dulcamara* and *Nicandra physaloides*. They arise in about the same manner as do the stomata of the Solanaceae as described earlier by Strasburger (24, p. 323) from epidermal cells which divide once to form the two guard cells. These mother cells are somewhat sunken below the level of the epidermis.

Minden found that more water pores were developed on the leaves of plants in damp situations than on these from drier locations.

In species like the potato the hydathodes with their water pores seem to be a development of the ordinary stomata (Fig. 7). The guard cells and the opening of the water pores of the potato are larger but structurally the two are identical and all intermediate types may be found on the young leaflets. No attempt has been made to follow the development of the internal structure of these hydathodes in their development, but the external appearance of the stomata and hydathodes is essentially the same. The statement that the water pores lose their ability to close is incorrect so far as the potato guard cells are concerned. Stomata

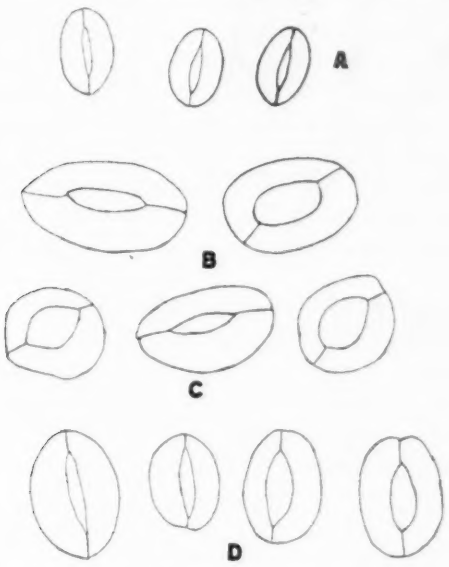

FIG. 7. A, Ordinary stomata, x300: B, C, and D, guard cells from hydathodes from three mature leaves.

from a practically full grown leaflet closed almost completely in a solution of 5 per cent glycerin, and the guard cells of the water pores behaved in a similar fashion. The guard cells do not seem to be involved in the browning of the tissue underneath the water pore in some cases, but in others these cells had suffered in a similar manner. The latter condition is to be expected if the injury is very severe.

The death of the tissues under the water pore begins at the tip end of the plant and proceeds backward under the pores on the sides of the leaflet. The pores along the basal margins are last to become involved if they ever are affected.

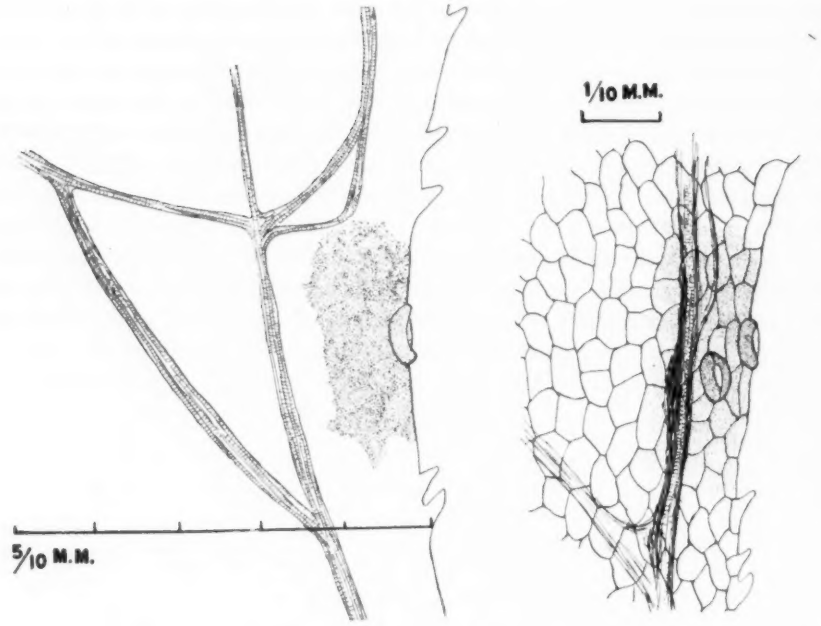

FIG. 8. Margins of mature leaflets, showing marginal vein and hydathodes. Dead tissue is indicated by the dotted areas.

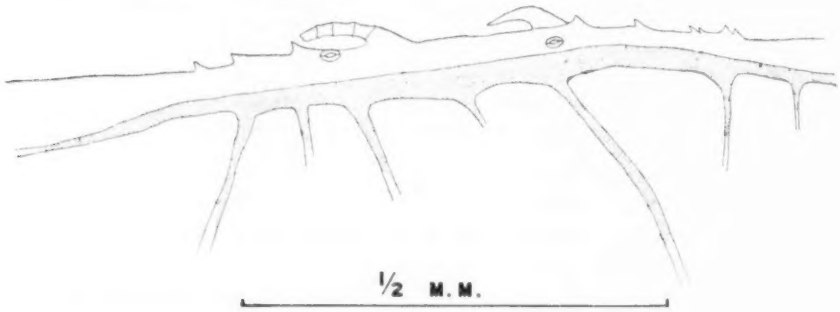

FIG. 9. Margin of leaf showing the extent of injury to the marginal amd connecting veins. Injury is indicated by dotting.

Figure 1.B displays the superficial aspect of tissue death in the tip of the leaflet. The palisade parenchyma under the openings turn brown and, since the hydathodes are very closely distributed in this region, the whole tip soon becomes thus discolored. The tissues involved on the side of the leaflet may include the palisade parenchyma and also

the pulp cells at the margin or over the marginal vein (Figs. 8, 9) without the bast of the marginal vein becoming injured. If, however, the water pores lie very close to the vessels of the vein, the bast and the long cells which accompany the veins become browned and apparently die, especially with the older leaves. Figures 8 and 9 are illustrations from mature leaves. The tissues around the hydathodes on the young leaflets seem to have a better chance to escape injury especially if they lie at the bottom of a depression or well on the margin (Fig. 5, C) but the water pores which open to the outside without any chamber above them (Fig. 5, B) may show browning. The young leaflets are never as susceptible to tipburn as the older ones, hence it is doubtful whether cell death seriously damages the plant in view of the fact that the influence is mainly local. Figures 8 and 9 exhibit the extent of the injury to the marginal vein and, of course, to the portions of the leaf which depend upon it for water supply and for the removal of the products of assimilation. It would seem from these measurements that the localized damage due to the presence of the water pores does not extend into the margin of the leaflet for the distance of more than 1 mm. or possibly even ½ mm. This theory would be correct if the influence of the marginal vein did not extend beyond its immediate proximity, but this is not true, as will be shown later.

The death of the cells located under the water pores would seem to be due to excessive transpiration leading to so severe a plasmolysis that they are able to revive and resume normality. However, Morse's (17) observations touching the effect of borax applied in the fertilizer upon the rapidity of tipburn attack and the progressive and early death of the leaflets at least raise the question whether other factors may not be at work to bring about similar results. He says:

"Quite a different type of injury occured upon all plants which were grown in pots (in the greenhouse) containing a fertilizer which carried borax.

"This type of injury was characterized by death and drying out of the tips and margins of the leaflets. The injury first appeared on the basal leaves and afterwards on the upper ones, and almost without exception was noted on the tips of the leaflets first and then on the margins. . . . In like manner the terminal and first two lateral leaflets were attacked first and were more severely affected. . . . . .

"The age of the leaf seemed to be a determining factor. A lower leaf might be badly affected while the leaves from a young shoot formed on its axil would appear entirely healthy at the same time. However, these leaves from the younger shoots nearer the base later showed the same marginal injury. . . . .

"The appearance of the affected leaves seemed to indicate simply a progressive death and drying out of the tissues. While there was a fairly distinct line of demarkation between the diseased and healthy portion of the leaves, the latter near this line usually showed more or less fading out of the normal green color to a lighter green or even a yellowish tinge. . . . .

"It seemed reasonable to suppose that compounds of boron were being taken up by the roots, were being carried along with dilute solutions of food materials and deposited in leaves. . . . . .

"The sample in the injured leaves gave a positive test (chemically) for boron while that from the healthy leaves gave a negative test."

Neller and Morse (18) have confirmed these borax results in an elaborate series of greenhouse experiments conducted at the Vermont Agricultural Experiment Station on a variety of plants.

Similar observations were made by the writer on the severe attacks following the use of a chemical compound in the potash which caused the plants to rot off before reaching the surface of the ground. This chemical was not borax nor any of the borax compounds according to the statement of the Chemist of the Vermont Agricultural Experiment Station and of the Chemists of the Bureau of Soils, of the U. S. Department of Agriculture, at the time, but was not identified.

Such occurences of course call for explanation. Spanjer (22, p. 75) having kept a plant of *Phaseolus multiflorus* for 24 hours in a 0.06 to 0.05 per cent solution of eosin, under pressure, noted that the guard cells of the water pores become colored and then collapsed and closed. If evaporation were rapid, the water would be quickly removed from the first faintly tinted drops and the percentage of dye in solutions would increase and even if the first drops which came through were not toxic, they might rapidly become so. A similar process probably goes on if solutions which contain traces of toxic substances such as the boron compounds are absorbed by the roots and are later extruded by the water pores. Even if the percentage of toxic substance were not high enough to kill the guard cells at once, the limits of toleration would soon be passed and the guard cells would be poisoned. The percentage of borax absorbed in the soil water from fertilizers maintaining traces of it must be exceedingly minute but in the margins of the leaf it is comparatively easy to obtain chemical tests for it.

It is possible, too, that even if the guard cells were not killed by toxic substances, they may be poisoned to such an extent that they are unable to close at times when water losses from evaporation become excessive. In fact, tipburn may be due to such a paralysis of these organs. Neigh-

boring fields apparently similar in all respects are very differently affected during a tipburn epidemic, and this suggestion would seem to offer an explanation of such an occurrence. In the writer's experience, however, the heaviest foliage losses occur on fields that are exposed to the direct rays of the sun, that is that slope toward the south, especially if they are so located that the unobstructed wind can sweep across them. It is his judgment that the toxic effect is likely to be secondary in most instances, although undoubtedly at times it is a primary factor.

Some of the older experiments by which liquids were forced through the water pores under pressure of a mercury column were repeated on branches of the potato plant. Under a 30 to 35 cm. pressure, it was possible to force water out of the pores in about two hours. Fair-sized droplets were formed, often five or six to a leaflet, and two or three droplets on the small intermediate leaflets. These droplets were rather evenly distributed along the margins. The distribution of the water pores is such as to have led one to expect that they would have tended to form toward the tip; however,the point of least resistance seems to be the determining factor, and this may be as well at the side or back of the leaflet as toward the tip. A very weak eosin solution was forced through the pores in two hours, but it was about 24 hours before the yellow color appeared. The leaf tissues were flooded with the solution, and the leaves drooped and wilted in a few hours afterward. No special region was noted as especially susceptible to flooding. A 2.5 per cent solution of copper sulphate was forced through in another plant, and the copper reaction was obtained in the drops within 24 hours. The branch thus treated suffered even more severely than did that treated with the eosin solution, and the leaves were black and practically dead at the end of 36 hours. Haberlandt's experiment was repeated, in which the margins were painted with a 0.1 per cent solution of mercuric chlorid in 5.0 per cent alcohol before being subjected to pressure. The margins promptly darkened, and the water collected along the margin in light greenish yellow drops. It is a moot point whether these drops were secreted through the pores or through ruptured leaf tissues. Spanjer (22, p. 75) was able so to poison the guard cells of the water pores of *Phaseolus multiflorus* with solutions of copper sulphate mercuric chlorid, or with iodin vapor that they collapsed and closed. The leaf tissues were filled with water in all their intercellular spaces, but only after 30 hours did water exude from the pores. The droplets which then appeared undoubtedly had broken through the epidermal tissues somewhere in the neighborhood of the water pores.

The marginal anastomoses which really form the marginal vein

probably play more of a rôle than its size would indicate although it is one of the largest of the anastomoses in the vascular system. This rôle is the equalization of the water supply to all parts of the leaf, since this vein comes into contact with all the lateral veins. Haberlandt (9) found that severing one or two of the principal veins in the leaves of the sycamore did not cause the death of those portions of the leaf supplied by these veins, since the tissues seemed able to derive their water supply from other sources by means of the abundant anastomoses. In fact, such leaves remained to all appearances uninjured, living as late in the autumn as did other leaves. However, he is careful to point out that while new tracheidal connections may be formed, such changes involve considerable delay, during which the portions of the plant which have been cut off from their regular water supply are in danger of drying up. Such a condition might occur in the potato leaf whenever a very hot

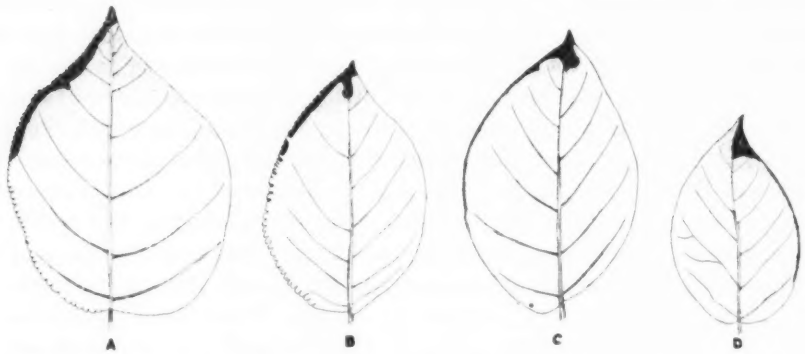

FIG. 10. A, B, Leaflets whose margins were clipped on August 25 and examined and drawn on August 29 after being exposed for four days to hot sunshine.

period intervened. These marginal tissues would be apt to die under the influence of the heat and the intense sunlight. Excessive transpiration in some one or more portions of the leaflet—as elsewhere described by the writer (12)—would necessitate an extraordinary water supply. The vessels which regularly serve these affected portions can not carry enough water; neither can a sufficient excess be brought by means of bypaths through the anastomoses of the marginal vein. As a consequence, the leaflet wilts, the cells are plasmolized and the chlorophyll and the chlorophyll bodies are destroyed. If the plasmolysis goes beyond a certain limit, the cells can not recover and local death ensues. An explanation of this sort would seem to account for the advance of tipburn beyond the margin of the leaf; and since in some cases physiological tipburn involves half or more of the entire area of the leaflet, some

adequate reason must be advanced since the damage immediately under the water pores is slight and localized.

On August 25, 1920, at 2 p. m. the marginal veins of a few Green Mountain potato leaflets were cut in about 20 places along one side of the margin only. The cuts were made with a safety razor blade and were not over 1 mm. long. The weather was intensely warm in the sun

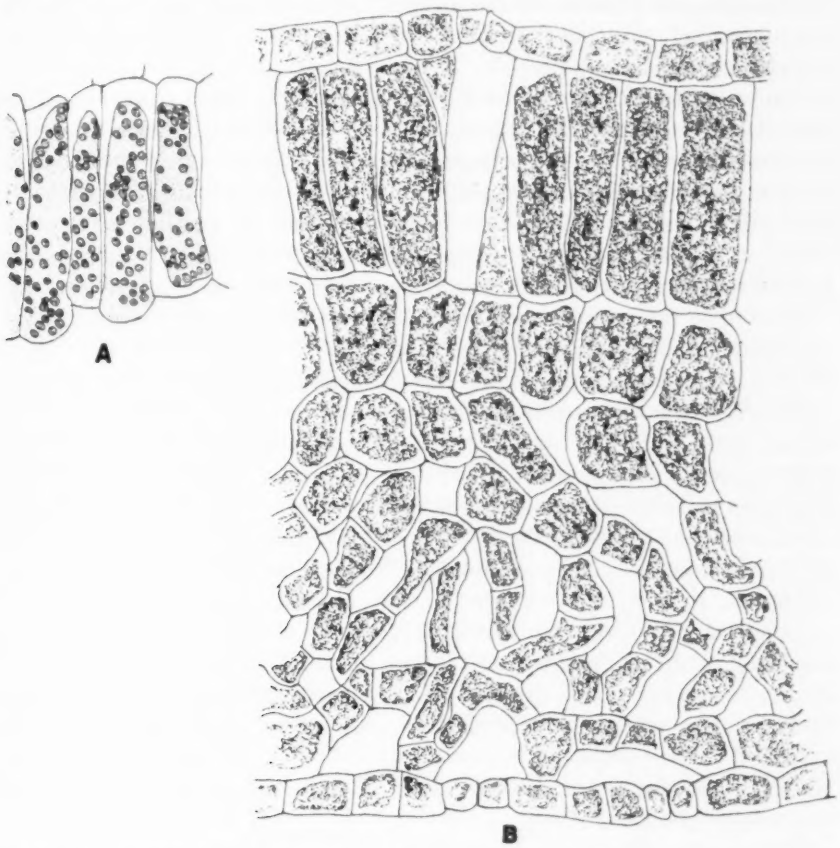

FIG. 11. Section from a living leaflet, showing the cells of the area wilted after a very hot day (July 22). A is from a leaflet not as severely wilted as B. B will not recover; A will be yellowed.

and the plants showed signs of wilting. These leaflets on August 29 showed typical brown tipburn along the cut margins as well as the distinctly yellow margin characteristic of typical tipburn (Fig. 10, A, B). Severing the marginal vein in a number of places at a critical time will lead to tipburn. A similar experiment was tried with other leaflets,

1 mm. of the margin being shaved off, with similar results (Fig. 10, C, D).

The sequence of events in the death of the margin of the leaflet is probably much more complicated than the foregoing experiment would indicate. The dead cells surrounding the vein serve as a barrier to the outward passage of the water from the vessels into the leaf tissues, and the latter gradually dies during hot weather. The margin of the leaf finally collapses when it becomes brown. The marginal vessels are choked, no longer act, and then we have the loss of the important regulatory function described above.

The condition of the plant during a severe tipburn attack has been elsewhere described, (12) but it may be well to recall the main features of this disease. Those portions of the leaf upon which the sunlight falls at right angles to the leaf surface become wilted and yellowed. The other portions escape but, following change in position of the sun, other margins and tips present themselves successively to the right angled sun's rays and in turn may become wilted, while these portions subjected to this condition earlier in the day may recover their turgidity. A section of the leaf taken at this time while it is wilted, (Fig. 11) shows all the cells plasmolyzed and to about the same extent. The question naturally arises: why does plasmolysis occur only in the portion of the leaflet upon which the sunlight falls perpendicularly? The explanation appears to be in the peculiar form of certain cells. The palisade parenchyma cells are long and narrow and are lined with chlorophyll bodies along the sides. These absorb the sunlight and protect the underlying pulp parenchyma cells. As long as the leaf can protect its pulp parenchyma, it does not wilt badly, but any prolonged exposure of its under tissues to clear, hot sunlight promotes transpiration to an extent that the plant is unable to transmit enough water to this localized region to maintain cell turgidity. The portions that are worst plasmolyzed die, while other parts less severely affected regain turgidity but may become yellowed as a result of the destruction of the chlorophyll. Sun plants are always lighter in color than are shade plants of the same species.

The potato plant seems peculiar in respect to the amount and extent of the injury to which it is subjected by tipburn of the physiological type. The serious damage is done when the sun's rays fall on the tips and margins of the leaflets at such an angle that they are parallel with the side walls of the long palisade parenchyma cells. Many field plants, such as the pea and bean, assume a "sun position" in which the margin of the leaf is turned toward the sun, thus protecting themselves against damage. The diurnal movements of

Helianthus are probably for the same purpose. Wiesner (26) has expressed this relation of strong sunlight to plants, especially the tropical species, in the following principle: The adaptation of the plant to the direct sunlight expresses itself in such a way that the green vegetative organs, i. e. the leaves, avoid all direct sunlight of great intensity and take up only direct light of lesser intensity. He cites *Robinia pseudoacacia* as an example of a plant which receives direct sunlight at right angles; that is to say, direct sunlight causes the leaves to turn their edges to its rays. Many tropical trees hold their leaves straight up in the air in order to avoid the direct sun's rays. The potato plant, however, seems to exhibit no such attitude. Unlike those mentioned it is unable to avoid these destructive perpendicular rays. Hence any portion of the leaflet upon which they fall must needs suffer until the movement of the sun alters the angle when, in turn, other portions of the leaf or plant may be thus affected. In the meantime, however, it often happens that the chlorophyll has been destroyed and the cells plasmolyzed to such a degree that they can not recover.

The ease with the older leaves become plasmolyzed is increased by their lowered osmotic pressure as compared to that of the stems. During these periods of intense sunlight, the plant is forming starch in abundance and the stem juices are loaded with sugar which is being transferred to the tuber for storage as starch. The osmotic pressure data obtained during 1918 (13) have been supplemented during the past two years as a result of further observations still unpublished, wherein it was found that the pressure in the stems often was approximately as great as in the leaves.

Certain further observations on the chlorophyll content of the cells may have some bearing on the ease with which the older leaves are affected by too intense sunlight. The young leaves in the center of the plant are much darker green, in early July before any signs of tipburn appeared, than are the older leaves that are beginning to droop. If like weights of each are taken, boiled, and their chlorophyll extracted in alcohol it will be found that the tip leaves solution, diluted twice or thrice, is as intensely green as that from the older leaves. The augmented chlorophyll content of these tip leaflets served as an additional protection against cell destruction.

In this connection, too, it may be of interest to note that much of the increase in size of the leaflets is due to swelling of the cells, as the following data show.

	Area (sq. mm.)	Length (mm.)	Breadth (mm.)
Epidermal cells from underside of tip of young leaflet	0.0045		
Stomata from underside of tip of young leaflet		0.0033	0.0026
Epidermal cells from underside of tip of old leaflet	.00115		
Stomata from underside of tip of old leaflet		.0039	.0027
Epidermal cells from upper side of tip of young leaflet	.0007		
Stomata from upper side of tip of young leaflet		.0036	.0026
Epidermal cells from upper side of tip of old leaflet	.00205		
Stomata from upper side of tip of old leaflet		.0045	.0031

The amount of chlorophyll in the young leaves being two or three times that of the old leaves, bulk for bulk, it would seem that the chlorophyll per cell content does not increase very much during the period of the leaf expansion.

A study of the leaflets which have been subjected to severe plasmolysis but which have apparently recovered shows that many do not attain normality but, on the contrary, are very susceptible to further excessive transpiration losses. A yellow or yellowish green region usually surrounds the brown and dead tissue and the chlorophyll is much less and the chlorophyll bodies are smaller.

If the leaves are cleared with glycerin, it is possible to observe the affected tissues. The plant hairs seem to succumb most readily, that is, they are more easily and more seriously plasmolized than any other tissue unless it be the bast of the veins. The veins which extend into the green tissue from the brown and dead area show a light brown bast along the vessels. Occasionally, on some leaflets, the stomata shows brown guard cells and the underlying tissue is killed for the distance of a few cells from the air chamber. Occasionally two stomata in close proximity to each other are connected underneath by dead cells along the air spaces which connect them (Fig. 12). However, these conditions are not often observed and the advance of the tipburn into the leaflet is to be expected along the veins. In a few instances, too, some of the irregular pulp parenchyma cells touching the bast are browned.

Sections of the leaflets from mature plants taken from the field during August were placed in 4.5 and 5.0 per cent solutions of potassium nitrate, the air was removed so far as possible by exhaustion with a pump, and the leaflets were examined after about an hour's immersion. The

cells of the hairs were found to be plasmolyzed severely, as were the sieve tubes and their companion cells. The irregular pulp parenchyma was slightly plasmolyzed, while the long palisade cells seemed to be almost unaffected. These facts tend to corroborate the theory that the death of the leaflet is due to extreme and repeated plasmolysis and wilting.

Particular care has been taken thus far in the discussion to avoid all mention of the injuries due to insects, especially the leafhopper. The reason for this silence has been that the only phase of the tipburn problem under consideration was physiological in its nature and not due to insects in any way. The almost entire absence of leafhoppers from Vermont fields eliminates them as a factor and makes the solution of the problem that much simpler. During the latter part of July and the early part

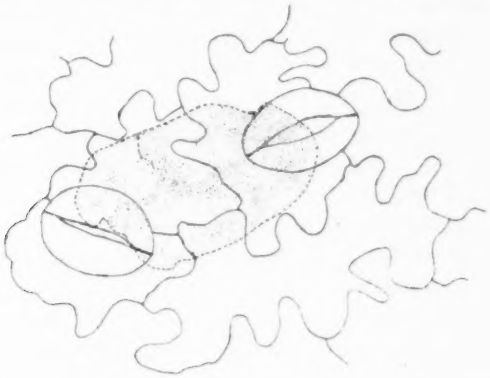

FIG. 12. Cells under adjacent stomata (killed portions indicated by dotting) but in an area that has apparently recovered from mild tipburn.

of August, one or two leafhoppers could be found on a plant if careful search was made, but in about a week (July 20 to 27,) the potato plants lost at least a third of their foliage from physiological tipburn. This fact in itself is sufficient answer to those who doubt the field occurrence of this type of tipburn. Similar weather was experienced in 1917, for example, and the same type of tipburn occurred.

During August, the number of leafhoppers continued to increase until 10 to 15 could be scared from a plant, but the tipburn remained almost stationary in extent. The weather was cool and the sunshine neither hot nor brilliant. A few days of warm weather in late August (20 and 27) brought about considerable addition to the tipburn area. The author believes that the presence, field importance, and physiological origin of tipburn has been proved.

On the other hand, the relation of the leaf hoppers to what has been called tipburn in regions where these insects are so abundant that they fly up in clouds when disturbed is not so clear. The experiments which the entomologists have made are all aside from this point, since they avoid or are unable to produce field conditions in the screened plants with which they have worked. Their usual procedure has been to put a single plant under a screen without leafhoppers and another plant beside it under a similar screen with them. Any field ecologist in botany would tell them at once that the intensity of the sunlight is greatly diminished under any sort of screen and that the wind velocity has been reduced to almost nothing. Both these factors reduce transpiration, and loss of water is the essential factor in tipburn of the type now under discussion. The vital question is: Would the plant with no leafhoppers tipburn physiologically if left under real field conditions? It would be hard to devise a procedure that would separate the two factors, but until the entomologists are able to do this, it must be assumed that physiological tipburn is the original type and that in most instances the leafhopper is only an aggravating and serious factor. Under similar conditions, the aphids might contribute in a similar manner, as is indicated in "The Report on the Occurrence of Insects and Fungus Pests on Plants in England and Wales" for the year 1919 (6) which says: Potatoes were noteworthy in 1919 as having suffered from a very general attack by aphids which was followed by various obscure troubles apparently correlated with the aphid attack. It has not yet been shown whether the progressive death of the tissues surrounding the original puncture injury is due to a toxin introduced by the aphid, but it seems likely, since the potato shows a very marked reaction to the toxin introduced by species of Capsids. Or, to go back still further, Smee (21) attributed all potato diseases to aphids, especially the blight which was at that time the subject of discussion and investigation, since the causal organism had not then been discovered. Smee describes similar diseases on turnips, black nightshade, belladonna, stramonium, horseradish, tomato, nettle, mallow, etc., all induced by these same active insects.

The type of injury attributed to the leafhopper is a puncture which partially severs some of the more important veins. The leaf collapses and, sooner or later, the lamina of the leaf supplied by the vessels dies and becomes brown, this browning area having the shape of a fan with the broad portion on the margin. According to various entomologists, it makes little difference how dark it is or at what time of year the trial is made. The injury is so severe that the leaflets gradually die until

the plant is only a bare stalk. It is a question whether the severance of a single vein, even of good size, would cause the death of the tissues which it ordinarily supplies with water, but if the connection is broken during very hot weather, when all the water tubes, working at full capacity can barely supply all parts of the leaf lamina, the tissues might well become plasmolyzed and collapse. In the former cases, the anastomoses would serve as substitutes, but in extremely hot weather these bypaths would not suffice.

Haberlandt's experiment in which he severed some of the large lateral veins was repeated on August 25, using several potato leaflets. The leaves were again examined on August 29 but nothing had happened, the tips, margins and portions of the lamina which are supplied with water by these veins being as alive and healthy as on August 25. The sunshine had been brilliant and the temperature high, but the anastomosing veins had kept the tissues supplied with enough water to prevent severe plasmolysis and death during a fairly critical period when tip burn was advancing.

The portion of the leaflet supplied by the vein that had been severed by the leafhopper puncture might appear to die from the insect attack and still the death might really be brought about by the physiological form of the disease; for during the weather which favors insect attack, physiological tipburn would undoubtedly make its appearance and break down the anastomoses, since field conditions so far as heat and sunshine are concerned are much the same throughout the United States. It is almost impossible to separate the two factors if they occur together, but it must be conceded that the injury which the leafhoppers do to the plants must be serious when it will produce a burning of the leaves in a cage in partial shade.

The yellowing of the chlorophyll in the region of a tipburn area is to be regarded as a physiological symptom, as the writer has already pointed out. Intense illumination will break up chlorophyll and increase the percentage of carotin and, so far as is known, the chorophyll is not able to regenerate itself (23, p. 92). This destruction of chlorophyll to form yellow pigment seems to be going on all at times in green plants in the sunshine, but those plants which have devised some means of preventing a too rapid destruction have survived. Sun leaves always exhibit a yellow-green hue as compared to the intense blue-green of shade leaves. The entire plant might be yellowed as a result of the sucking of the plant juices by insects, but it is hardly likely that the yellowing would be limited to a line bordering the dead area.

An experiment was described in a previous paper by the writer (12)

in which tipburn was produced in a very short time by the exposure of greenhouse plants to the action of an intensified sunlight produced by a series of three mirrors. This was done in April, obviously a time of year when tipburn does not occur on such plants. Similar experiments were conducted during the following spring with a somewhat different arrangement of mirrors. These mirrors, each 2 feet long, were so placed one above the other in a frame that they could be tilted. It was thus possible to subject a leaflet for at least a half hour to an almost threefold intensity of sunlight. The burns that were produced simulated in many ways the browning brought about by sunlight and heat in late July, but with some slight differences which had not been noticed in the previous paper. Any portion of the leaflet could be subjected to the intensified light and plasmolyzed to such a point that recovery was impossible. The leaflets showed brown areas over at least a part of the treated regions. These brown areas, however, were rather sharper in these margins than in natural tipburn produced in the middle of the summer, the typical yellow margin being absent.

The tipburn that appears early in the season partakes of the nature of this artificially produced scorching. After a season of lush growth, with tender foliage produced during fairly cool weather with an abundance of moisture, a few hours of hot, brilliant sunshine will scorch almost any portion of the plant upon which it may happen to fall directly for any length of time. Such a period was noted during the present year about July 3. The damage done was considerable but was not to be compared with that which came on about two weeks later.

The writer, therefore, is inclined to revive the distinction heretofore made by some of the older writers and to recognize two forms of physiological injury to the potato plant due to heat, sunlight, and excessive transpiration. The one type is caused suddenly and disappeared abruptly, presenting rather clear lines of demarcation and attacking even the younger, succulent leaves. The other type is the result of several days of warm, dry sunshine, usually shows tissues surrounding the dead portion that are diseased and appear yellow, and is more common on the middle-sized and older leaves. Intermediate forms undoubtedly appear, and there really is very little essential difference in them, since extreme plasmolysis is at the root of the injury in either instance. In tipburn, however, the plasmolysis is repeated and its influence extends somewhat beyond the area where it causes death.

The stomata on the potato leaf undoubtedly play an important rôle in the transpiration of water; hence some attention was given to these organs as well as to the water pores. De Vries (25, p. 605–506) sa y

in translation: "The epidermis of the potato leaf bears stomata both above and below, though on the lower side considerably more than on the upper side. The number per square millimeter varies according to the environment, so that at times the upper surface is found to be entirely without stomata. Czech (4, p. 842) found 0–2 per square millimeter, while I have found on one specimen out of the garden an average of 10 and on some other plants grown from seed, 20 stomata on the same area. On the under side Morren (16) and Czech (4) agree on 263 stomata per sq. mm. It would not be impossible that here, also the environment has something to do with the number of stomata, as Czech has observed the fact that the varieties which grow in damp situations have more stomata than related species which occur in dry places. I have found the end length of the stomata to be 0.045 mm."

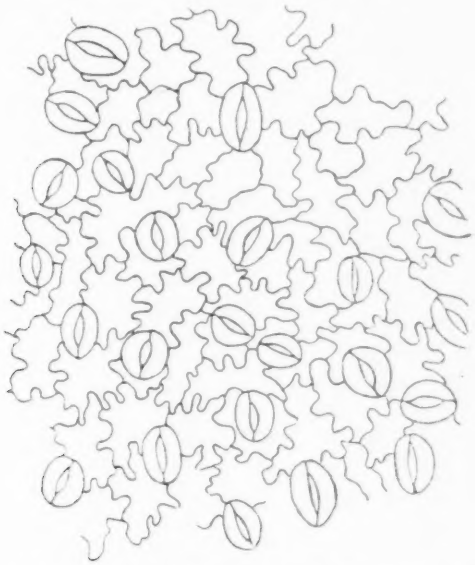

FIG. 13. Upper side of young leaflet: 230 stomata in 1 sq. mm.. x200.

The counts given below are from Green Mountain potatoes growing in a rather dry soil during a very dry summer (1921), the counts, with one exception (Sept. 2) being made during August. Tip leaflets were used (Figs. 13, 14, 15).

	Stomata per square millimeter	Stomata on an average leaflet
Young tip leaflet:		
Under side, middle region	300	82,800
Upper side, middle region	230	52,900

Medium size tip leaflet
Under side.....400.....348,000
Medium size tip leaflet
Upper side:
Middle region.....140.....
Basal region.....80..... } 95,700

Large size tip leaflet:
Under side:
Basal region.....115.....
Apical region.....105..... } 242,000

Upper side:
Basal region.....60.....
Apical region.....30..... } 99,000

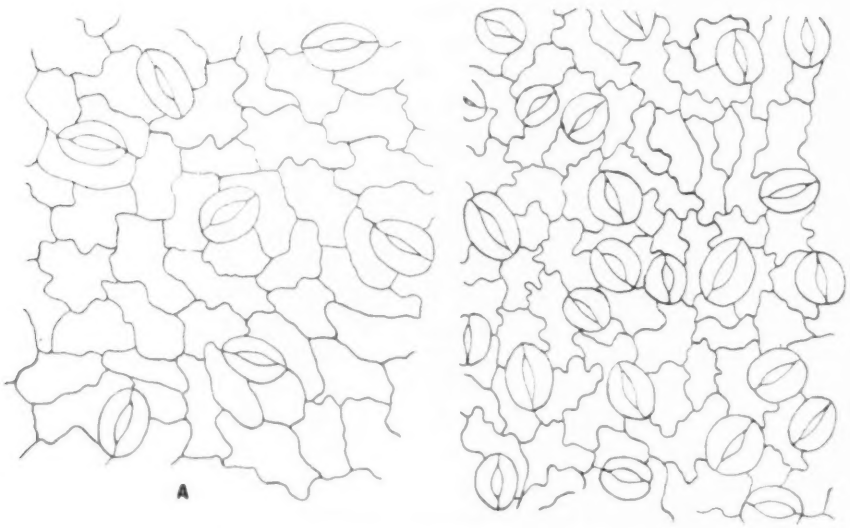

FIG. 14. A. Upper side of medium-sized tip leaflet with 140 stomata in 1 sq. mm. x200. B. under side of medium-sized tip leaflet with 400 stomata in 1 sq. mm. x200.

Clearly the numbers vary on different portions of the leaflet, a very large proportion being located on the upper side of the leaflets. On the young leaflets 39 per cent are on the upper surface and 61 per cent on the lower on the medium sized leaflets, 21 per cent on the upper and 79 per cent on the lower; while on the large tip leaflets the percentages are respectively, 20 and 71. The young leaflets are held upright at a

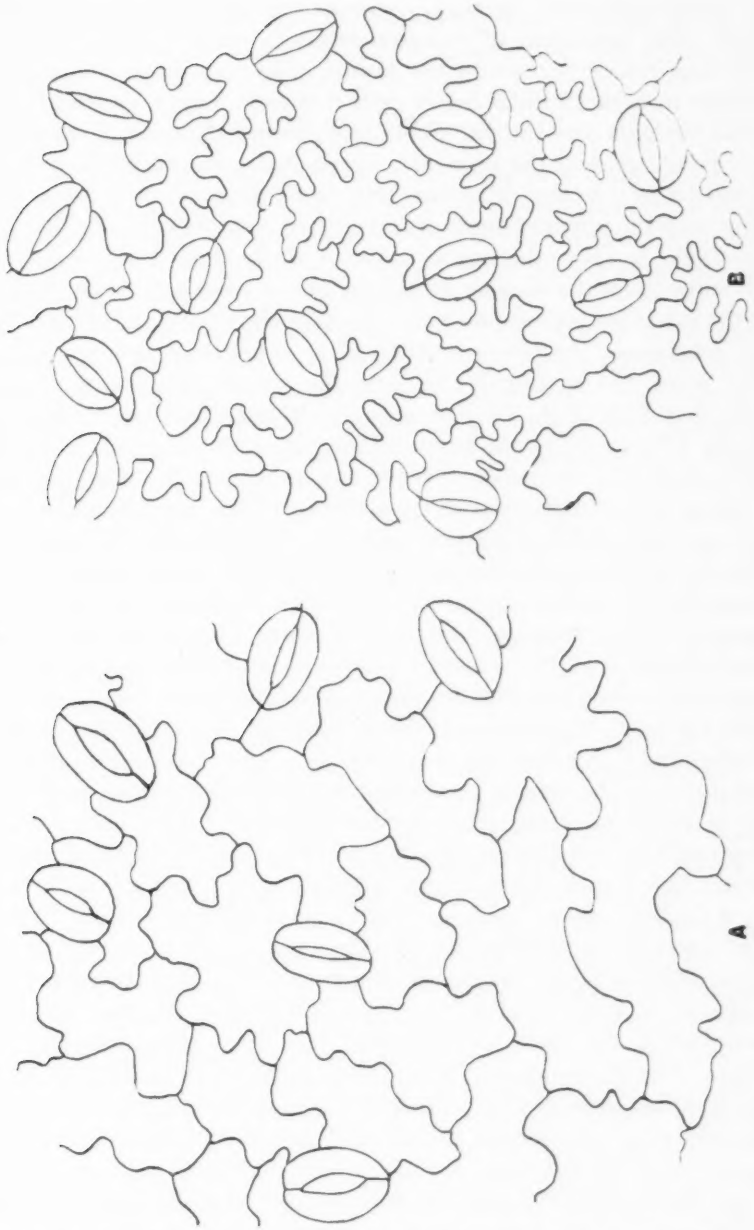

FIG. 15. A. Upper side of old tip leaflet, near base of lamina with 60 stomata in 1 sq. mm. x200. B. under side of old tip leaflet, near the base of lamina with 115 stomata in 1 sq. mm. x200.

very acute angle to the sunlight, whereas the medium and large leaflets droop. The formation of stomata seems to cease on the upper side some time before it does on the lower. The young leaf in its growth increases in breadth much faster than it does in length, so that the leaf lamina expands and the tip of the leaf instead of being shaped like a spear point assumes the form of a broad oval. In this connection it is interesting to note that Miss Rea (20) found about three times as many stomata on the under surfaces of leaves from normal shoots of *Campanula rotundifolia* L. as on the upper, while the shade shoot leaves have more than three times the number on the under side as compared to the upper and the sun shoot leaves show numbers approximately equal on both sides.

In conclusion, the relation between the practice of spraying and the water pores, the marginal vein, and the tipburn and margin-burn to which they lead might be pointed out, although this has already been done by Clinton (3) in the paper previously cited. The gelatinous films which constitute bordeaux mixture flow down to the edge and tip of the leaf and effectually stop up the air pores. It is very doubtful whether they can open at all when they are thus sealed up by the thick layer which is usually found around the margins of the leaflets. It constitutes a hard and fairly permanent deposit, comparable in a way to limestone, rather than to the sediment which Clinton (3) has in mind. Lime-sulphur forms no such thick and tough layer. Its very fine granules or crystals are of no avail in stopping up the water pores and hence would not act as a deterrent in the early stages of physiological tipburn. In view of the fact that the pores are always located on the upper side of or just over the margin toward the upper side of the leaf, such a stoppage is possible, whereas if they were located on the under side the spray could not reach them and they would remain open. The Bordeaux mixture also covers a large part of the stomata which lie on the upper side of the leaf—about one-fifth of them are thus located—and the loss of water must be considerable when they are in active operation.

The shading effect of Bordeaux mixture has been discussed by a number of writers. It should be remembered that this shading is most marked along the veins where the mixture tends naturally to flow and to dry. The importance of this fact is readily seen when it is recalled that the bast cells of the veins and the neighboring pulp parenchyma succumb when the wilting in localized areas becomes so marked that the cells are plasmolyzed to a point that they can not recover. The denser shade probably helps at these points. The shading also helps in providing the plant with a screen through which the sun's rays must filter before affecting the chlorophyll. Hence the destruction of the

chlorophyll to form carotin would be retarded and the light which entered the palisade cells, instead of falling on straight lines, would enter them in a diffused condition and the damage to the underlying tissues would undoubtedly be less.

SUMMARY

1. The tipburn discussed in this paper is entirely distinct from that form due to insect injury, such as the hopper burn due to the attacks of leafhoppers. Such insects are very rare in Vermont fields during the time when tipburn is at its height. This type is associated with hot, dry weather and clear, brilliant sunshine.

2. Potato leaves are provided with hydathodes around their margins but especially toward the tip. These hydathodes resemble the stomata but are placed so as to open directly on the vessels of a large vein which runs close to the margin of all the leaflets. A group of these hydathodes is located just at the tip of each leaflet where many of the vessels of the marginal vein end.

3. Tipburn begins beneath these hydathodes especially at the tip of the leaflets. The death of the tissues under the terminal water pore group leads to the browning and shriveling of the extreme tip of each leaflet. The tissues die under the water pores along the side of the leaflet and apparently break the continuity of the water supply system of the marginal vein.

4. The futher advance of the tipburn into the leaf is due to direct sunlight acting on the cells of the leaf leading to such an extreme plasmolysis that the cells are not able to recover. Associated with this plasmolysis is the destructive action of the sunlight upon the chlorophyll bodies and the chlorophyll itself. This expresses itself in the yellowing of the green portion of the leaf in the region dead from tipburn.

5. In certain cases, such as poisoning from borax compounds in fertilizers, the death of the cells under the water pores is undoubtedly the result of an accumulation of the toxic salts in or around them in the intercellular spaces. It is possible, also, that the toxic effect is more marked on the guard cells of the water pores and that they are unable to function normally, that is to close or open.

6. A larger number of the stomata are located on the upper surface of the potato leaf than is generally supposed, varying from about one-third on the young leaves to less than one-fourth on the older ones. The tipburn seems to have little effect on the stomata or the tissues under them. Although occasionally they function in the browning and death characterizing this malady, as a rule stomata can practically be disregarded in the advance of the tipburn.

7. Another type of tipburn, more in the nature of a scorch, seems to occur especially on the young succulent foliage. This type may be seen at times in June or early July whereas the type described above is more common after July 20 in this region and is at its height about August 10. This form of tipburn may be produced by excessive sunlight in the laboratory at any time by the use of mirrors.

8. The injured tissue in the portion of a leaflet which seems to have recovered from tipburn is the long bast and companion cells and some of the adjacent cells of the pulp parenchyma.

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LITERATURE CITED

(1) ARTSCHWAGER, E. F. Anatomy of the potato plant, with special reference to the ontogeny of the vascular system. Jour. Agric. Res. **14**: 221–252. 4 fig., pl. 27–47. 1918. Literature cited, p. 251–252.

(2) BARY, ANTON DE. Comparative anatomy of the vegetative organs of the phanerogams and ferns. XVI. 659 p., illus. 1884.

(3) CLINTON, G. P. Spraying potatoes in dry seasons. Connecticut Agric. Exp. Sta. 33d–34th Ann. Rpt. [1909]–10: 739–752. 1910.

(4) CZECH, KARL. Ueber die functionen der stomata. Bot. Ztg. **27**: 801–809, 817–823. 1869.

(5) FENTON, F. A. Progress report on the season's work on the production of potato tipburn. Jour. Econ. Entomol. **14**: 71–83. Fig. 2–3. 1921.

(6) GREAT BRIT. MIN. AGRIC. AND FISHERIES. Intelligence Dept.—Plant Pests Branch. Report on the occurrence of insects and fungus pests on plants in England and Wales for the year 1919. 68 p. 1921. (Great Brit. Min. Agric. and Fisheries, Misc. Pub. 33).

(7) HABERLANDT, GOTTLIEB. Anatomisch-physiologische Untersuchungen über das tropische Laubblatt. II. Über wassersecernirende und-absorbirende Organe. Sitzber. K. Akad. Wiss. [Vienna], Math. Naturw. Kl. Bd. **103**, Abt. 1: 489–538. 3 pl. 1894.

(8) ———— Zur Kenntniss der Hydathoden. Jahrb. Wiss. Bot. [Pringsheim], Bd. **30**: 511–528. Pl. 22. 1897.

(9) HABERLANDT, GOTTLIEB. Physiological plant anatomy, translated from the 4th German edition by Montagu Drummond. XV, 777 p., 291 fig. London. Notes, p. 704–755. 1914.

(10) HARTZELL, ALBERT. Further notes on the life history of the potato leafhopper. (*Empoasca mali* Le Baron). Journ. Econ. Entomol. **14**: 62–68. Fig. 1, pl. 1. 1921.

(11) JOST, LUDWIG. Lectures on plant physiology; authorized English translation by R. J. Harvey Gibson. XIV, 564 p., 172 fig. Oxford, England. 1907. Bibliographies at end of lectures.

(12) LUTMAN, B. F. Tip burn of the potato and other plants. Vermont Agric. Exp. Sta. Bul. 214. 28 p., 9 fig., 2 pl. 1919. Bibliography, p. 28.

(13) ———— Osmotic pressures in the potato plant at various stages of growth. Amer. Jour. Bot. **6**: 181–202. 2 fig. 1919. Literature cited, p. 202.

(14) MINDEN, MAX VON. Beiträge zur anatomischen und physiologischen Kenntniss Wasse-secernierender Organe. 76 p., 7 pl. Stuttgart. 1899. (Bibliotheca, Bot., Bd. 46).

(15) MOLL, J. W. Untersuchungen über Tropfenausscheidung und Injection von Blättern. Versl. en Meded. d. Koninkl. Akad. v. Wetensch. Amsterdam II, 15: 237–337. 2 pl. 1880.

(16) MORREN, EDOUARD. Détermination du nombre des stomates chez quelques végétaux indigènes ou cultivés en Belgique. Acad. Roy. Belg. Bul. Cl. Sci. **16**: 639–659. 1863.

(17) MORSE, W. J. Some observations upon the effect of borax in fertilizers. Maine Agric. Exp. Sta. Bull. 288: 89–120. Fig. 14–27. 1920.

(18) NELLER, J. R. AND W. J. MORSE. Effects upon the growth of potatoes, corn and beans resulting from the addition of borax to the fertilizer used. Soil Sci. **12**: 79–105. Pl. 1–13. 1921. References, p. 104–105.

(19) NESTLER, ANTON. Untersuchungen über die Ausscheidung von Wassertropfen an den Blättern. Sitzber. K. Akad. Wiss. [Vienna], Math. Naturw. Kl. Bd. **105**, Abt. 1: 521–551. 2 pl. 1896.

(20) REA, M. W. Stomata and hydathodes in *Campanula rotundifolia* L. and their relation to environment. New Phytol. **20**: 56–72. 6 fig. 1921. References, p. 72.

(21) SMEE, ALFRED. The potato plant, its uses and properties: together with the cause of the present malady. XXXVII, 157 p., 1 fig. New York. 1847.

(22) SPANJER, OTTO. Untersuchungen über die Wasserapparate der Gefasspflanzenn Bot. Ztg. Bd. **56**, Abt 1: 35–81. Pl. 3. 1898. Autoren-Verzeichnis, p. 79.

(23) STAHL, ERNST. Zur Biologie des Chlorophylls. Laubfarbe und Himmelslicht Vergilbung und Etoilement. **154** p., 4 fig., 1 col. pl. Jena. 1909.

(24) STRASBURGER, EDUARD. Ein Beitrag zur Entwicklungsgeschichte der Spaltöffnungen. Jahrb. Wiss. Bot. [Pringsheim], Bd. **5**: 297–342, pl. 35–42 (partly col.). 1866–67.

(25) VRIES, HUGO DE. Beiträge zur speciellen Physiologie landwirthschaftlicher Culturpflanzen. V. Wachsthumgeschichte der Kartoffelpflanze. Landw. Jahrb. Bd. **7**: 591–682. Pl. 16–17 (col.). 1878.

(26) WIESNER, JULIUS. Uber die Anpassung der Pflanze an das Diffuse Tages und das directe Sonnelicht. Ann. Jardin Bot. Buitenzorg, Sup. 3: 47–60. 1910.

RHIZOCTONIA SOLANI AS A POTATO-TUBER ROT FUNGUS

M. SHAPOVALOV

WITH PLATE XXIII

Though a well recognized parasite of the potato plant, *Rhizoctonia solani* Kühn is not ordinarily thought of as the cause of any type of tuber rot. Indeed, it is difficult to induce this organism to decompose any appreciable quantity of normal healthy potato-tuber tissues when inoculated with pure cultures. Various forms of Rhizoctonia injury have been reported as occurring in nature, but none could properly be called rot or decay. Nevertheless, there is good evidence at hand to justify the inclusion of this widely distributed soil organism in the list of potato-tuber rot parasites. However, it is only under special environmental conditions as well as in special abnormally constituted parts of the host that this decay takes place. So far, it has been observed by the writer only in irrigated sections of the West and only on elongated pointed-end tubers of the Netted Gem and Burbank varieties. The abnormal stem ends of these tubers (occasionally also knobs and eye ends) appear to be susceptible to the Rhizoctonia infection. When the latter takes place, a very peculiar jelly-type decay develops.

Carpenter[1] and Pratt[2] attributed the so-called jelly-end rot primarily to *Fusarium radicicola* and *F. oxysporum*, indicating, however, that other factors may in part be responsible. It is true that various forms of wet stem-end rot prevail in the irrigated soils of the West which are quite thoroughly infested with several parasitic species of Fusarium. Naturally, these fungi may be most frequently found associated with stem-end rotting tubers, chiefly as primary, but occasionally as secondary invaders. Yet, cases are not infrequent, especially at harvest time, when elongated Burbanks or Netted Gems show stem-end decay of the jelly type while being entirely free from the Fusarium infection. Isolations from such tubers have shown that *R. solani* is the only parasitic organism present.

During the surveys of western potato diseases in the summers of 1920 and 1921, the writer had an opportunity to collect various stages of

[1] Carpenter, C. W. Some potato tuber-rots caused by species of Fusarium. Jour. Agric. Res., **5**: 183–209, pls. A, B, XIV-XIX. 1915.

[2] Pratt, O. A. A western field rot of the Irish potato tuber caused by Fusarium radicicola. Jour. Agric. Res., **6**: 297–309, pls. XXXIV–XXXVII. 1916.

the jelly-end rot on Burbanks in California and on Netted Gems in Idaho. Special care was given to select tubers which came from healthy vines and had no vascular discoloration. The consistency of such decay was distinctly jelly-like. The color in the first stages of the infection was nearly white, but as the decay developed it turned yellow and then light brown and finally brown. All the isolations from such jelly-rot specimens of the pointed stem ends yielded *R. solani*. Portions of the decaying tissues under the microscope showed the cells to be permeated with the mycelium of the fungus. This Rhizoctonia jelly rot does not usually advance very far into the tuber, but stops at a certain definite distance which varies for different tubers and apparently is determined by the extent of the abnormal elongation of the stem end. When this limit is reached, a sharp division between the healthy and the diseased tissue may be seen. The decayed end may be sloughed off when the tuber is just taken from the ground or it may dry up, shrink and harden (Pl. XXIII figs. A and B).

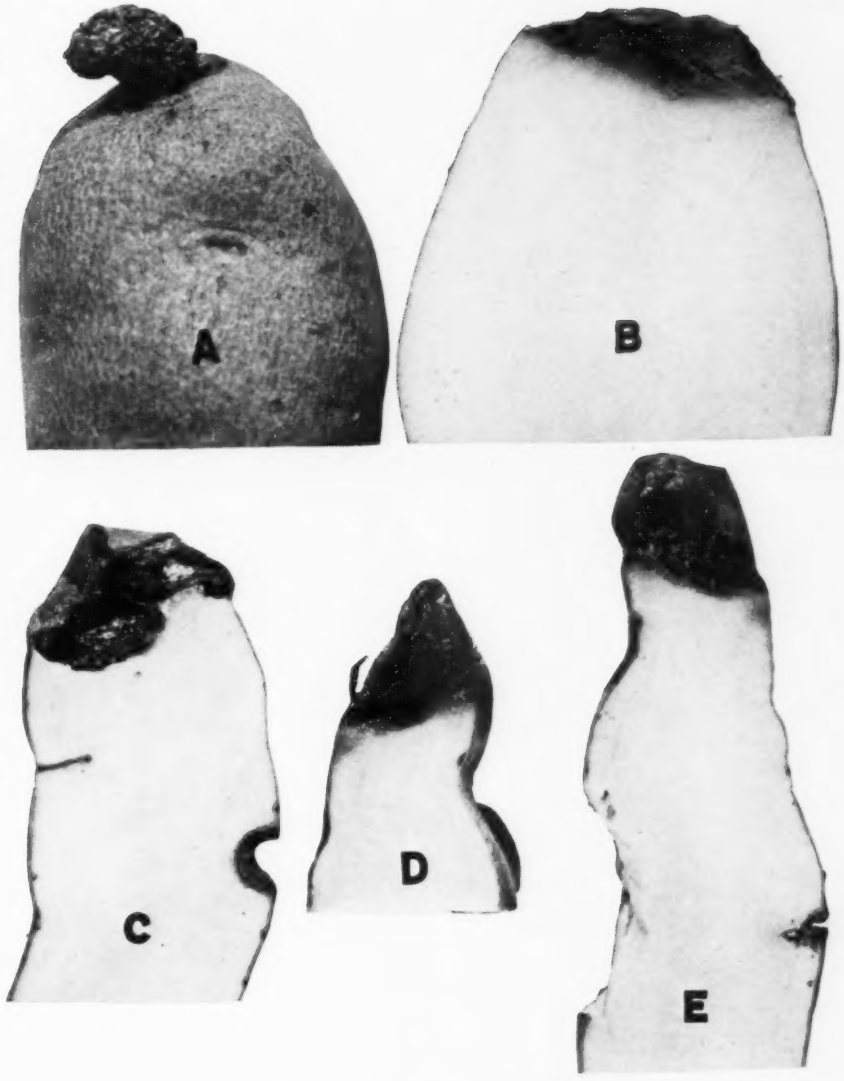
The flesh of the elongated stem ends, when cut open, differs from the remaining tissues of the tuber by a watery and somewhat translucent appearance. Under the microscope sections of these areas reveal a striking deficiency in starch contents of the cell. These stem ends may remain free from any infection, but they lose water in storage more rapidly than the rest of the tuber and subsequently shrivel up, though no decomposition of the tissue takes place. With regard to their internal appearance the elongated starch-free stem ends resemble most closely firm seed pieces found after the growth of the plant has been completed and all or most of the starch has been utilized. Such seed pieces, too, very often become affected with a jelly type of decay. Specimens of of this kind have been found by the writer in the vicinity of Washington, D. C., and in the greenhouses of the U. S. Department of Agriculture and species of Fusarium, Vermicularia, and Rhizoctonia have been isolated from them.

To ascertain further the possibility of a causal relationship between *R. solani* and the jelly type of decay of the elongated stem ends of the potato tuber, the following inoculation experiment was carried out. A thick layer of cotton was placed on the bottom of a glass moist chamber and covered with several layers of filter paper. Both the cotton and the filter paper were thoroughly saturated with boiled hot water and allowed to cool. Following this 5 abnormally elongated Netted Gem tubers, previously disinfected in 1 per cent formalin solution for 1 hour, were inoculated with *R. solani* isolated from the jelly rot material collected in the West in 1921. The inoculation was made both at the extreme

stem ends and on the sides, corresponding respectively to the abnormal and the normal tissues of the potato. Slits were made at these two points of each tuber and the Rhizoctonia mycelium from two-days old cultures on cooked potatoes was inserted in these slits. The inoculated tubers were then placed on the wet filter paper in the moist chamber described above and all were completely covered with wet sterilized sand. The chamber itself was left uncovered. During the first 10 days the tubers were kept in a refrigerator at night and in the laboratory room during the day at a temperature of 20°–25° C after which they were exposed for an additional 7 days in the laboratory during the day and night time. In this manner the material was subjected to all the variations in temperature such as may exist in nature. On the 17th day the tubers were examined and found to have each about 2.5 cm. of jelly-like decay at the stem ends and only a slight amount of soft but not jelly-like rot at the side inoculations (Pl. XXIII, figs. C, D, and E). *R. solani* was recovered from the jelly rot of the stem ends.

The results of this inoculation experiment as well as field observations and cultural work with field specimens show very clearly that *R. solani* is an important causative agency in bringing about the jelly type of decay of elongated stem ends of Burbanks and Netted Gems in the West, occasionally knobs and eye ends also being subject to the infection. Of course, this fact does not exclude the possibility of other organisms, particularly *Fusarium spp.*, causing a similar form of decay. Apparently, the jelly-like consistency is determined more by certain abnormalities of the host tissue, conspicuously manifest by a very low starch content or its entire absence than by the species of the parasite. So far as *R. solani* is concerned the extent of the abnormal structure of the tuber determines the progress of the decay, while Fusarium may advance further as a storage rot. The jelliness of the decayed portions disappears shortly after harvesting. The jelly-rot areas when dried and shriveled are externally indistinguishable from other forms of stem end rot, such as those caused by various species of Fusarium and in certain cases by the blackleg bacillus.[1] Consequently, it is rather misleading to apply the term "jelly-end rot" to any form of potato tuber decay either in storage or in transit and the broader term "stem-end rot" should be preferred in all those cases. Jelly rot or jelly-end rot designates an unstable form of field decay only. Soon after the tubers are put in sacks or in storage cellars this trouble passes into a general class of stem-end rot.

[1] Shapovalov, M., and Edson, H. A. Blackleg potato tuber rot under irrigation. Jour. Agric. Res. 22: 81–92. 1921.



JELLY-TYPE ROT CAUSED BY *Rhizoctonia solani*:

A and B—Natural infection in the field, specimens photographed 5 months after harvesting: the decay was arrested and the diseased stem ends became shriveled and dry.

C, D, and E—Result of artificial inoculation with pure culture of *R. solani*, 17 days after the inoculation; C and E show also a very slow progress of the decay in the side noculations.

UNIV. OF MICH.

THE RELATION OF SOIL MOISTURE AND SOIL TEMPERATURE TO BUNT INFECTION IN WHEAT.

CHAS. W. HUNGERFORD

WITH FIVE FIGURES IN THE TEXT

INTRODUCTION

Bunt, or stinking smut, is one of the most serious problems in the wheat growing sections of the Pacific Northwest. Nowhere else in the United States and probably nowhere in the world, with the possible exception of certain parts of Australia, are the annual losses from bunt as great as they are in the Palouse region of Idaho and adjacent Washington. In this region winter wheat is grown extensively, summer fallowing is practiced and there is a small amount of rainfall during the summer months. Due to these climatic conditions and cultural practices, the soil becomes infested with windblown spores of the bunt organism *Tilletia tritici* (Bjerk.) Wint. at threshing time. If the condition of the soil is favorable for germination of these spores immediately before or at the time of seeding, a very smutty crop may result although the seed may have been carefully treated.

In 1919, in coöperation with the Office of Cereal Investigations of the United States Department of Agriculture, a survey was made of cereal diseases in all of the grain growing counties of Idaho. In the counties where soil infestation by the bunt organism is known to take place, there was as high as 85 per cent infection in some fields. The average losses from this disease in these counties varied from 5 to 14 per cent of the total production. Some years the loss has been even greater.

It has been known for a number of years that soil contamination by wind-blown bunt spores is practically universal in the Palouse region. More recently it has been demonstrated that this condition exists in other regions as well. Barss (1) in Oregon and Mackie (12) in California have reported that soil infestation by bunt is common in certain parts of each of these states. The writer has found during the last three years that a like condition prevails in certain counties in southern Idaho where summer fallowing is practiced.

VARIOUS METHODS RECOMMENDED FOR OVERCOMING SOIL INFECTION.

Various cultural practices have been recommended as aids in preventing infection from the soil. Heald and Woolman (6) in 1915 recommended, first, seeding before the threshing begins or if this is not possible

at least before the fall rains, second, replowing the summer fallow after the first fall rains, and third, late planting. Heald (5) suggests that under certain conditions it may be better to grow spring wheat instead of winter wheat, as spring wheat is not subject to infection from the soil. Heald and Zundel (7) recommend also crop rotation where summer fallow is not necessary for conservation of soil moisture and shallow seeding, as additional preventative measures. These recommendations have been made as a result of observations and experiments carried on at Pullman, Washington.

REVIEW OF RECENT INVESTIGATION UPON THE RELATION OF SOIL TEMPERATURE AND SOIL MOISTURE IN INFECTION BY VARIOUS FUNGI.

Within the last few years the question of the relation of the temperature of the soil to infection by various fungi has received considerable attention. Jones (9) calls attention to the importance of this line of investigation and reviews some of the more important literature. Gilman (3) has also reviewed the literature upon this question and states that *Fusarium conglutinans* Woll., would not produce the characteristic symptoms of cabbage yellows unless the temperature was above 17° to 22° C. Tisdale (14) working with flax wilt, Johnson and Hartman (11) with the root rot of tobacco, and Richards (13) with the Rhizoctonia disease of potatoes, have shown that there is a very marked influence exerted by the temperature of the soil upon infection by the specific organisms with which they were working. Jones (10) in 1895 called attention to the fact that soil temperature plays an important part in the amount of oat smut which may develop from a given seed lot.

Güssow (4) called attention to the influence of soil temperature upon infection by *Tilletia tritici* as indicated by certain field observations made by him in Canada. Woolman (16) in working with the same disease concludes:

"First, smutted grain planted untreated in smut-free soil, when the mean soil temperature is above 65° F. and sufficient moisture present to cause quick germination will produce a practically smut-free crop. Second, under the same conditions the per cent of smut will increase with the fall of temperature from 60° to 45° F., at which point the smut per cent is highest. Third, below 40° F. the smut per cent decreases with the fall of the temperature."

Jones (9) quotes Humphrey as stating, for the same disease, that "Soil temperatures of 0° to 5° C. and above 22° C. are decidedly unfavorable to infection." Walker and Jones (15), in a study of the relation of soil temperature to onion smut, found that under controlled

greenhouse conditions a large percentage of plants grown on smutted soil were infected at soil temperatures ranging from 10° to 25° C. A reduction in infection was noted at 27° C. and complete freedom from the disease resulted at 29° C. They also found that in out-of-door plantings a gradual reduction of infection occurred as the season advanced and the soil temperatures rose.

Although considerable work has been done in recent years in regard to the influence of soil temperature upon infection by various pathogenic organisms in the soil, very little attention has been given to the influence of the amount of soil moisture upon the development of such organisms. Heald and Woolman (6) in calling attention to the effect of the amount of moisture in the soil at planting time upon infection by the spores of *Tilletia tritici*, state, "Our experiments have given some evidence that planting when there is just sufficient moisture to induce germination is a good practice, and even that dry planting and waiting for a rain is better than planting in a very wet soil." Mackie (12) states, "Bunt spores require about 14 per cent of moisture in the soil or a moist atmosphere for germination" and that "soils may be moist enough to sprout the wheat while too dry to germinate bunt spores." Walker and Jones (15) have shown that soil moisture is not a limiting factor in the development of the onion smut fungus, *Urocystis cepulae* Frost. At a very high or very low moisture content they found a reduction in the amount of smut but this reduction was associated with a decrease in seed germination and rate of growth of the onion plants.

EXPERIMENTAL DATA

That the amount of moisture in the soil at planting time may have a very marked effect upon the amount of bunt in wheat has been shown in a striking way by observations which have been made in Idaho during the last 5 or 6 years. In the summer of 1919, Mr. A. E. Wade, at that time County Agricultural Agent in Lewis County, Idaho, called the writer's attention to observations which he had made. He observed several instances where there was a small amount of smut in part of a field, which had been seeded in dry soil before a rain, while in the balance of the field, seeded with the same seed after a rain, there was a much higher percentage of smut. A specific example cited by Mr. Wade follows. A part of a field which was seeded October 22 in dry soil produced only one per cent smut. Rain fell during the night of October 22, not enough, however, to keep the farmer from seeding again the next day. The same seed was used in completing the field

October 23 and this portion of the field produced 30 per cent smut. A number of similar cases have come to the writer's attention during the last 3 years.

The writer had endeavored to test under controlled conditions the influence of both soil moisture and soil temperature upon infection of wheat by *Tilletia tritici*. The following data give the results of these experiments.

METHODS

Jenkins Club wheat was used in all the experiments. This wheat is the most popular and the highest yielding wheat in northern Idaho, and is fairly susceptible to bunt. Duplicate soil samples were always taken at the depth the wheat was planted. Moisture determinations were made on a dry weight basis and the moisture equivalent is given for each different kind of soil used. The soil used in the greenhouse experiments was in each case composed of Palouse silt loam to which was added a small percentage of fine river sand. The moisture equivalent of this mixture was 20.7. The moisture equivalent of the soil in the field plots which were used was found to be 27.2. The moisture equivalent[1] was determined by the method given by Briggs and McLane (2).

In experiments where the soil was artificially smutted, spores were secured by grinding up smut balls and sifting the spores through a fine screen. The smut spores thus secured were thoroughly mixed with the soil before planting. In all greenhouse experiments and where soil containers were used in the field the soil was removed from the containers to a depth of 2½ inches and a uniform amount of smut was thoroughly mixed with each lot of soil before planting.

FIELD EXPERIMENTS

In the spring of 1919 an experiment was started at Nez Perce, Idaho, and duplicated at Moscow on the University Farm. Six soil containers were filled with soil containing different amounts of moisture varying from near saturation to less than enough to cause good germination of wheat. Large road tiles 3 feet long and having an inside diameter of 14 inches were used at Nez Perce, and galvanized iron cans of about the same size were used at Moscow. These were sunk in the ground so that the tops were just above the surface of the surrounding soil. The soil was heavily smutted and Jenkins Club wheat which had

[1] The writer is especially indebted to Professor Guy R. McDole, of the Department of Agronomy of the University of Idaho, for advice in connection with this work and for the actual determination of the moisture equivalent of the soils used.

been rolled in viable spores of *Tilletia tritici* was planted in each container. Soil moisture samples were taken from each container at planting time and again when the wheat had all emerged. The average of these two was used as the average moisture content of the container for the experiment. A canvas was spread over the tops of the containers in order to keep evaporation at the minimum. The graph in

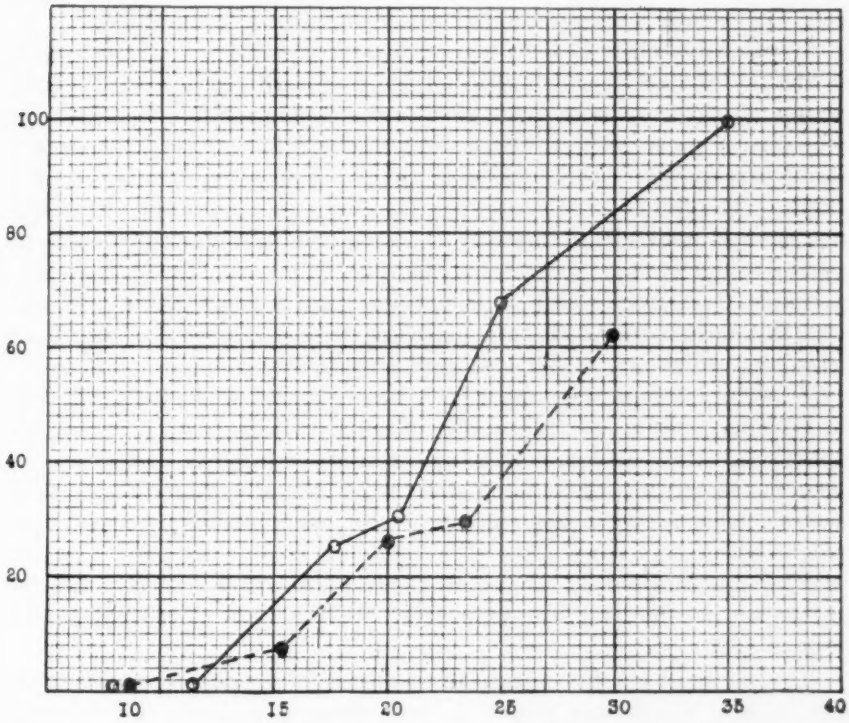


Fig. 1. Abscissa shows percentage of moisture in the soil at planting time. Ordinates the percentage of bunt infected plants. The unbroken and broken lines represent the results of the experiments at Moscow and Nez Perce respectively.

figure 1 gives the results of the experiment.[1] The soil temperature varied about 3 or 4 degrees F. in the several containers. The dryer soil had a higher temperature in each case. At Moscow the soil temperature varied from 48° to 60° F. during the time of germination of the wheat. At Nez Perce the variation was from 42° to 60° F.

Twelve circular plates 1½ inches in diameter were made of Plaster of Paris and viable spores of *Tilletia tritici* were placed on the flat sur-

[1]A brief abstract of this experiment has already been published. (8).

face of these plates. These were tied together in pairs and a pair buried in the soil in each soil container used in the above experiment at Moscow. When the wheat had emerged these plates were taken out and the spores were examined for germination. No germinating spores were found on the plates from cans numbers 1 and 2. On the plates from can number 3 a very few germinating spores were found; on those from cans numbers 4 and 5, slightly better germination was found; and about 25 per cent of all spores were germinated on the plates from can number 6.

An extensive series of tests was outlined in the fall of 1919 and again in the fall of 1920 in which series of rod-row plantings and one-fortieth acre plantings were to be made at intervals during the fall when various amounts of moisture were in the soil. It was impossible to complete these experiments either year due to rather unusual weather conditions. The fall of 1919 was one of the driest on record and there was not enough moisture in the soil to cause good germination of wheat until late in October. Numerous plantings which were made, however, germinated in part where sufficient moisture was available. Whenever this early germination took place less smut developed than in wheat from seed which laid in the dust until after the rains began. Soil moisture determinations were made in a large number of fields in the fall of 1919 on farms in several counties of northern Idaho at the time when these fields were seeded. Although the data secured from this source were not by any means complete due to the lack of germination in early seeded fields, nevertheless, all the notes accumulated indicate that where wheat was sown after threshing had begun and after the soil had become infested by wind-blown bunt spores, the less the moisture in the soil at the time of germination, the less bunt developed in the crop of 1920.

One series of rod-row plantings was made on a piece of summer fallow ground which was especially well situated and which contained more moisture than the average soil. This series germinated fairly well and table number I gives the result of this experiment. Treated Jenkins Club wheat was used.

A Planet Jr. hand planter was used in making these rod-rows plantings and every effort was made to simulate field practices as much as possible.

The fall of 1920 was even less favorable for experiments of this nature. After September 10 there was no time in the fall when the average soil contained less than 15 per cent moisture. The ground was too wet for seeding during much of the time after that date.

TABLE I

The effect of soil moisture and cultivation upon bunt infection.

	Series I* Percent of Smut	Series II* Percent of Smut
(a) Ground not cultivated before planting.....	8	3
(b) Ground cultivated before planting.....	10	4
(c) Soil smutted, ground not cultivated.....	50	8
(d) Soil smutted, ground cultivated.....	55	15
(e) Seed smutted before planting.....	75	30

* Planted Sept. 1—Soil Moisture 16 per cent.
** Planted Sept. 25—Soil Moisture 10 per cent.

GREENHOUSE EXPERIMENTS

In order to test the effect of both moisture and temperature of the soil at planting time upon the amount of bunt in wheat, means were perfected for controlling both moisture and temperature of the soil within certain limits in greenhouse experiments. Three different ranges of temperatures were tried. The first, ranging from 9 to 12° C. was secured by means of a galvanized iron tank through which water was circulated. The second, ranging from 25 to 28° C. was secured by means of an electrically heated and controlled glass chamber. For the third room temperature which varied from 17 to 25° C. during the experiment was employed. Four lots of soil were used with moisture content as follows: No. 1, 13 to 14 per cent; No. 2, 16 to 17 per cent; No. 3, 18 to 23 per cent; and No. 4, 28 to 32 per cent.

The plants were grown in four-gallon jars. Bunt spores were added to the soil and Jenkins Club wheat, which had been mixed with viable bunt spores, was planted 1½ inches deep in each jar. The soil was kept at constant moisture content by covering the jars with empire cloth until the wheat had all germinated and emerged. Even in the series where the soil contained the least moisture, drops of water collected on the under side of the cloth and on the soil. It is the author's opinion that there was probably more germination of bunt spores in soil kept in a humid atmosphere than there would have been in a well aired soil.

Livingston porous cup soil irrigators were tried as a means of holding the soil at constant moisture content. These were not satisfactory as the writer was not successful in holding the moisture content of the soils used below 15 per cent.

TABLE II

Effect of soil moisture and various soil temperatures upon infection of wheat with Tilletia tritici.

No.	Moisture	Temperature, degrees C.	Per cent Smut
Series No. 1.			
1-1	14	9 to 12	40
2-1	17	9 to 12	71
3-1	22	9 to 12	90
4-1	32	9 to 12	19
Series No 2			
1-2*	13	17 to 25	25
2-2.	16	17 to 25	20
3-2	18	17 to 25	21
4-2	32	17 to 25	0
SeriesNo. 3.			
1-3	14	25 to 28	5
2-3	17	25 to 28	0
3-3	23	25 to 28	3
4-3	28	25 to 28	0

* Water accidentally leaked into this jar.

Table number 2 indicates clearly the influence of both moisture and temperature of the soil on bunt infection. It will be noted that in No. 4 of each series where the soil approached a state of saturation at 28 to 32 per cent moisture little smut was developed (Fig. 2). The soil used in the greenhouse was a mixed soil with a moisture equivalent of 20.7. As shown above in connection with field experiments it was found that 100 per cent bunt developed in wheat where the soil at the time of germination of the seed contained 35 per cent moisture. This was in field soil, the moisture equivalent of which was 27.2. These results show the value of finding the moisture equivalent of each soil in order to obtain a physical constant for purposes of comparison.

Figure 3 illustrates the effect of high soil temperature with the different soil moistures; figure 4 the effect of low soil temperature with the various soil moistures, and figure 5, the effect of high soil moisture with the various soil temperatures.

LENGTH OF LIFE OF BUNT SPORES IN THE SOIL

Woolman (16) has shown that bunt spores which have lain over winter on the open ground in wheat heads at Pullman, Washington, may retain their power to infect in the spring. Heald and Woolman (6) conclude: First, that the infection power from separate spores is

FIG. 2. Illustrating the effect of nearly saturated soil upon bunt infection.

Number	Percentage moisture	Temperature, degrees C.
4 /1	32	9 to 12
4 /2	32	17 to 25
4 /3	28	25 to 28

The bundles marked H contain healthy heads. Those marked S contain smutted heads.

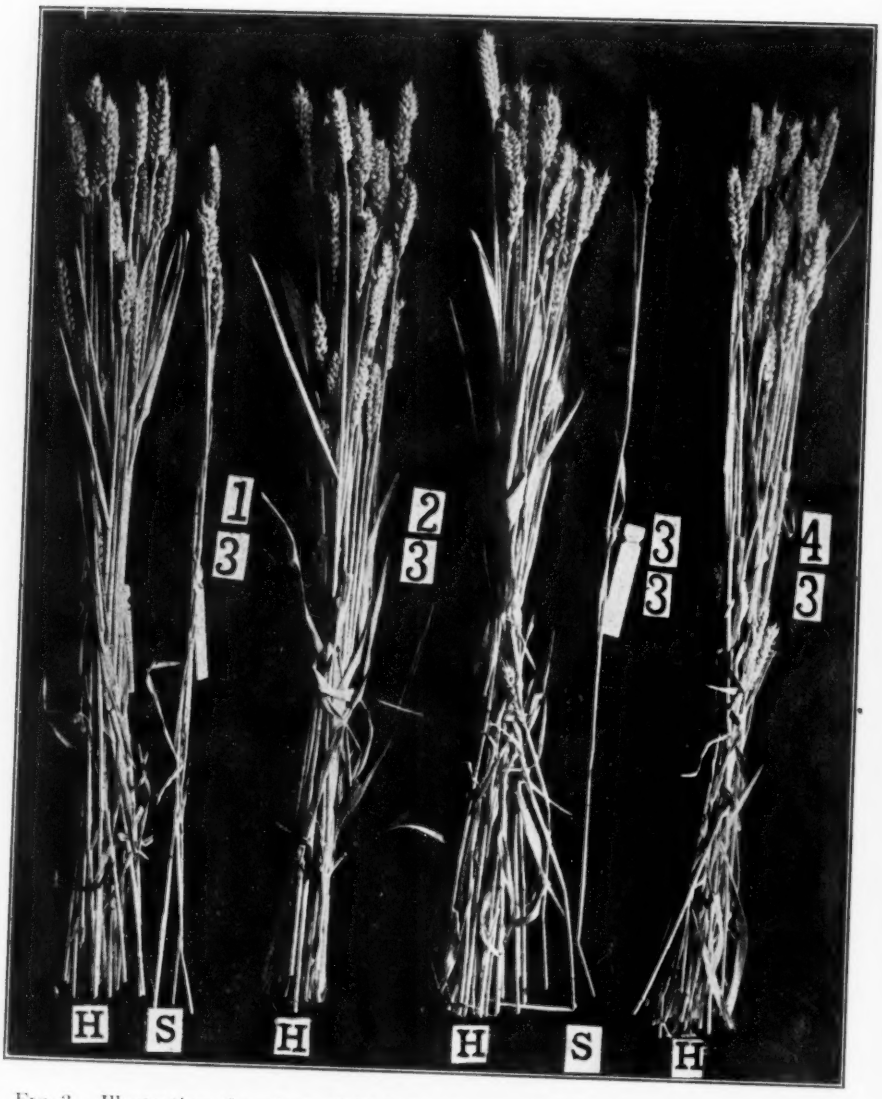


FIG. 3. Illustrating the effect of high soil temperature with various amounts of moisture in the soil.

Number	Percentage moisture	Temperature, degrees C.
1 /3	14	25 to 28
2 /3	17	25 to 28
3 /3	23	25 to 28
4 /3	28	25 to 28

The bundles marked H contain healthy heads. Those marked S contain smutted heads.

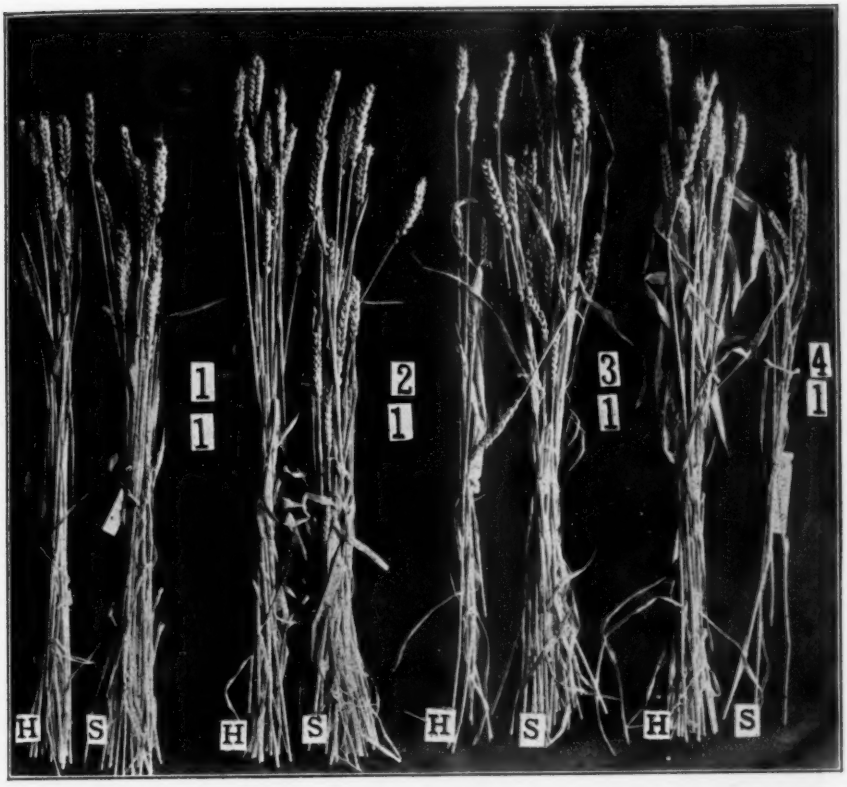


FIG. 4. Illustrating the effect of low soil temperature and various amounts of moisture in the soil.

Number	Percentage moisture	Temperature, degrees C.
1 /1	14	9 to 12
2 /1	17	9 to 12
3 /1	22	9 to 12
4 /1	32	9 to 12

The bundles marked H contain healthy heads. Those marked S contain smutty heads.

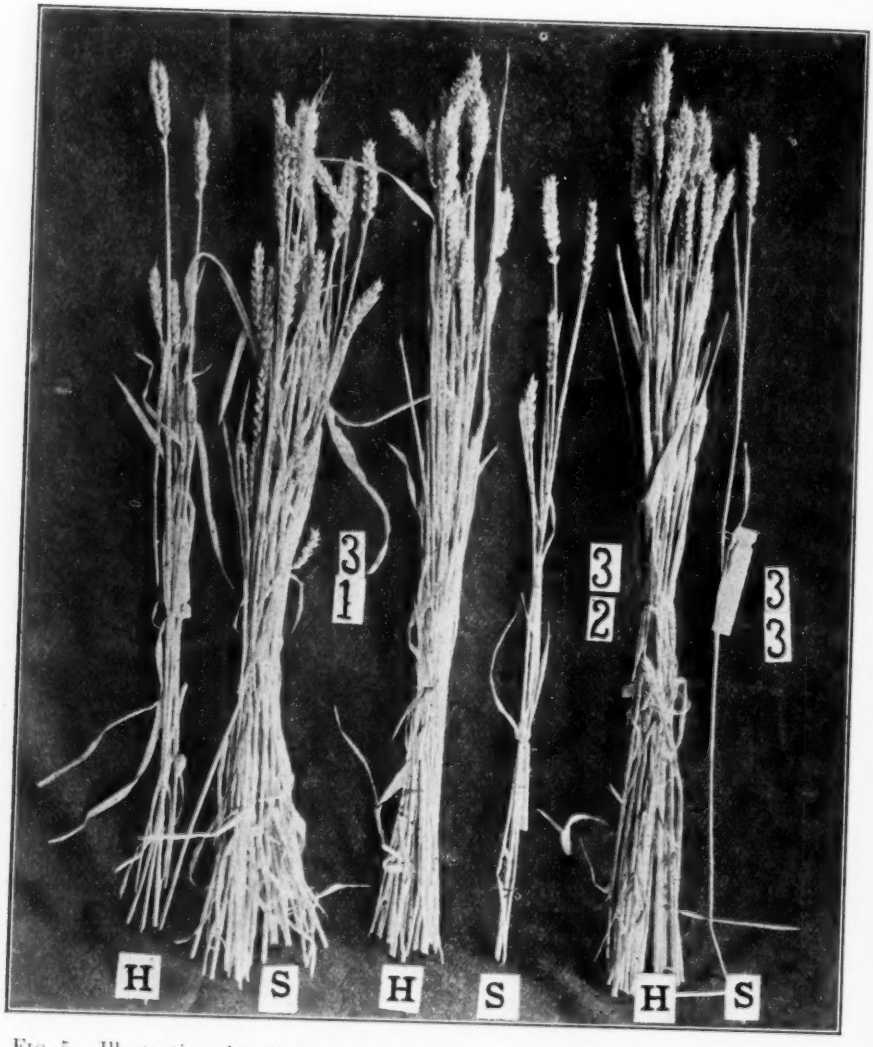


FIG. 5. Illustrating the effect of various temperatures with high moisture content in the soil.

Number	Percentage moisture	Temperature, degrees C.
3 /1	22	9 to 12
3 /2	18	17 to 25
3 /3	23	25 to 28

The bundles marked H contain healthy heads. Those marked S contain smutty heads

limited to 2 or 3 months in moist soil, and, second, that the spores in unbroken balls may retain their vitality for one year or more under natural field conditions. Güssow (4) reports experiments which tend to show that bunt spores may survive very low temperatures, even remain viable after being frozen in a block of ice. If, however, they have started to germinate, freezing will destroy their power to continue growth.

In the fall of 1920 a series of experiments was started to determine, first, the length of time bunt spores in the soil will remain viable under various conditions of soil moisture, and, second, the effect of cultivation upon bunt infection from the soil. The ground was uniformly and thoroughly smutted September 4 by scattering bunt spores over the surface. The ground was then divided into 4 plots one rod square. Each plot was treated as follows: Plot No. 1 was watered thoroughly every 3 days and cultivated the day after watering. Plot No. 2 was watered thoroughly before the first planting and then cultivated before each later planting. To Plot No. 3 no water was applied and the ground was cultivated before each successive planting. To Plot No. 4, no water was applied and the ground was not cultivated.

Successive plantings were made in each plot September 4, 11, 24, and October 2. Jenkins Club wheat was used which had been treated with bluestone by the standard method, by dipping in a solution of 1 pound of bluestone to 5 gallons of water for 10 minutes.

Soil moisture tests were made in each plot at each planting and after each watering or rainfall. Water was applied to the plots which were watered the day before the wheat was planted. In each case where watering was done the soil samples were not taken for several hours after the water was applied so as to allow for distribution of the moisture through the soil. The temperature of the soil was also taken at these intervals. Table No. 3 gives the results of this experiment.

TABLE 3

Effect of soil moisture and cultivation upon the length of life of bunt in the soil.

	Plot 1. Wet continually. Cultivated.		Plot 2. Wet at beginning. Cultivated.		Plot 3. Dry. Cultivated.		Plot 4. Dry. Not cultivated.	
	Moisture	Per cent Smut	Moisture	Per cent Smut	Moisture	Per cent Smut	Moisture	Per cent Smut
Sept. 4	20	30	22	35	10	19	10	23
8	22	—	20	—	10	—	10	—
11	24	10	23	35	17	14	18	8½
14	28	—	20	—	18	—	18	—
24	22	4½	21	13	20	6	20	5
Oct. 2	20	2	20	0	18	4½	19	3

Rainfall on September 11 amounting to over 0.25 inch interfered somewhat with the experiment. Doubtless the results would have been much more striking if no rain had fallen between the successive plantings. The numbers at the top of the table refer to the 4 plots listed above, the dates to the time of planting, and to the time moisture determinations were made. The moisture content taken on the dates indicated is given as the percentage of moisture in the soil and was computed on a dry basis as in previous experiments. The percentage of bunt was figured on the basis of the number of infected plants in the resulting crop. Soil temperatures varied from 50° to 70° F. during the period from September 16 to October 2.

SUMMARY

The control of bunt or stinking smut is one of the most difficult problems in the Pacific Northwest where the soil becomes infested with the spores of *Tilletia tritici* blown by the wind from threshing machines and combines.

It has been known for a number of years that soil contamination by wind-blown spores is almost universal in the Palouse region. More recently it has been shown that this condition exists in other regions as well.

Field observations in northern Idaho have shown that there is a very definite relation between the amount of moisture in the soil at seeding time and the amount of bunt which will occur in the resulting crop of wheat. Numerous cases have been observed where part of a field sown in dry soil produced a crop of wheat containing only a trace of bunt and where the rest of the field sown with the same seed after it had rained produced a very smutty crop.

Wheat was grown at Moscow, Idaho, in 6 soil containers filled with bunt infested soil varying in moisture content from 8 to 32 per cent at the time of planting and with a moisture equivalent of 27.2. The amount of bunt which developed in these containers varied from none to 100 per cent. The per cent of bunt increased progressively as the percentage of soil moisture increased. This experiment was repeated at Nez Perce, Idaho, with similar results.

Numerous field observations and field plot experiments tend to show that during the time when the soil is infested with viable spores of *Tilletia tritici*, the amount of moisture in the soil at planting time has a direct influence upon the amount of bunt in the resulting wheat crop.

Greenhouse experiments under controlled conditions have shown that low soil temperatures and a fairly high percentage of moisture in the

soil are both conducive to stinking smut infection. The highest percentage of infection was secured at temperatures ranging from 9° to 12° C. (48° to 54° F.) and in soil containing 22 per cent moisture and with a moisture equivalent of 20.7.

Under greenhouse conditions an exceedingly high percentage of moisture in the soil seemed to inhibit infection.

Some bunt infection was secured when the soil was held at a temperature of 25–28° C. (77° to 82° F.) during the germination of wheat.

Preliminary experiments appear to indicate that spores of *Tilletia tritici* in the soil loose their power to infect rather rapidly when the soil is moist and is cultivated frequently. Very little infection took place from spores which had been in the soil one month under the above conditions.

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LITERATURE CITED

(1) BARSS, H. P. Grain smuts and their control. Third Crop Pest and Horticultural Report, Oregon Agric. Exp. Sta. **1915-20**: 197–202. *Fig. 60–63.* 1921.

(2) BRIGGS, L. J. AND J. W. MCLANE. Moisture equivalent determinations and their application. Proc. Amer. Soc. Agron. **2** (1910): 138–147. *2 fig.* 1911.

(3) GILMAN, J. C. Cabbage yellows and the relation of temperature to its occurrence. Ann. Missouri Bot. Gard. **3**: 25–84. *21 fig., pl. 1 and 2.* 1916. Bibliography, p. 78–81.

(4) GUSSOW, H. T. Smut diseases of cultivated plants, their cause and control. Canada Dept. Agric. Central Exp. Farm Bull. 73. *57 p. Fig. 1, pl. 1–9.* 1913.

(5) HEALD, F. D. The stinking smut of wheat. Washington Agric. Exp. Sta. Popular Bull. 115. *15 p. Fig. 1.* 1918.

(6) ——— AND H. M. WOOLMAN. Bunt or stinking smut of wheat. Washington Agric. Exp. Sta. Bull. 126. *24 p. 5 fig.* 1915.

(7) ——— AND G. L. ZUNDEL. The control of cereal smuts in Washington. Washington Agric. Exp. Sta. Extension Dept. Bull. 72. *21 p. 8 fig.* 1921.

(8) HUNGERFORD, C. W. AND A. E. WADE. Relation between soil moisture and bunt infection in wheat. (Abst.) Phytopath. **10**: 53. 1920.

(9) JONES, L. R. Soil temperatures as a factor in phytopathology. Plant World **20**: 229–237. *2 fig.* 1917. Bibliography, p. 236–237.

(10) JONES, L. R. Some observations regarding oat smut. Vermont Agric. Exp. Sta. Ann. Rept. **9** (1895): 106–112. 1896.

(11) JOHNSON, JAMES AND R. E. HARTMAN. Influence of soil environment on the rootrot of tobacco. Jour. Agric. Res. **17**: 41–86. *2 fig., pl. 1–8.* 1919. Bibliography, p. 85–86.

(12) MACKIE, W. W. Seed treatment for the prevention of cereal smuts. Univ. Cal. Agric. Exp. Sta. Circ. 214. *8 p.* 1919.

(13) RICHARDS, B. L. Pathogenicity of *Corticium vagum* on the potato as affected by soil temperature. Jour. Agric. Res. **21**: 459–482. *4 fig., pl. 88–93.* 1921. Bibliography, p. 481–482.

(14) TISDALE, W. H. Relation of temperature to the growth and infecting power of Fusarium lini. Phytopath. **7**: 356–360. *Fig. 1, pl. 11.* 1917.

(15) WALKER, J. C. AND L. R. JONES. Relation of soil temperature and other factors to onion smut infection. Jour. Agric. Res. **22**: 235–261. *Fig. 1, pl. 25–27.* 1921.

(16) WOOLMAN, H. M. Stinking smut in wheat. Washington Agric. Exp. Sta. Popular Bull. **73**. *8 p.* 1914.

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